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The Persistence of DDT in a Forest Soil

BY
GEORGE M. WOODWELL

THE AERIAL APPLICATION of DDT to forests for the control of the spruce budworm (*Choristoneura fumiferana* Clem.) has brought concern lest the DDT accumulate after successive applications and produce undesirable side effects on the forest community. The persistence of DDT in crop soils has been well established in recent studies by Lichtenstein and others (1957, 1959) and in many earlier studies, some of which have been reviewed by Brown (1951). The present study, designed to discover the extent to which DDT accumulation occurs in an undisturbed forest soil after spraying for the budworm, is basic to a more extensive study of the direct effects of DDT on the trees of the spruce-fir forest.

Soil samples were taken from a forest community adjacent to the Budworm City Airport in north central New Brunswick in an area sprayed annually for control of the spruce budworm between 1952 and 1958. The vegetation is second-growth spruce-fir with balsam fir comprising 75 percent of the basal area, black spruce 13 percent, white spruce 8 percent and paper and yellow birch about 4 percent. The canopy is closed. The soil is a Plaisted loam.

A total of four pounds of DDT per acre was applied from the air during the period 1952-1958. This spray was applied at the rate of 1 lb per acre in 1952 and ½ lb per acre in subsequent years, making a total dosage of 4 lbs per acre in the six-year span. Technical grade DDT was mixed with oil at the rate of 1 lb DDT per gallon of oil to form the spray.

Soil samples were collected in July 1958, from six points within the stand. Four soil pits were dug approximately 30 feet from each sample point and the samples collected were composite samples made up from these four pits. Totals of one square foot of the A_{00} horizon, ½ square foot of the A_0 horizon, and one quart each of the A_2 and B_2 horizons were collected at each point. The subsoil samples taken in each pit were composites of the B_{2_1}, B_{2_2} and B_{2_3} horizons. Bulk densities of mineral soil horizons were determined from undisturbed samples collected with a Lutz sampler. Analyses for DDT were done in the Department of Chemistry, University of Maine, using benzene extraction and the Schechter-Haller method (1945). The data were kept separately by soil horizons for each of the isomers of DDT.

Results of these analyses, averaged for the six points and expressed as pounds of DDT per acre, appear in Table 1. The total amount present in the summer of 1958 was $0.459 \pm .090$ lb/acre. This total was made up of $0.156 \pm .026$ lb/acre of the para-para isomer and $0.303 \pm .086$ lb/acre of the ortho-para isomer, or about twice as much ortho-para as para-para.

Analysis of the spray used in the 1958 spraying indicated that these isomers occurred in that spray in the approximate proportion of 3:1, respectively, a ratio which agrees with published data concerning tech-

The author is Assistant Professor of Botany, University of Maine, Orono. This paper is a Conservation Foundation Study: part of a study of the effects of DDT on succession in the spruce-fir forest. Manuscript received Dec. 20, 1960.

TABLE 1. Means of DDT analyses completed for soils of six sampled points near Budworm City, New Brunswick. Figures are in pounds per acre.

Soil		Isomers of DDT		
Horizon	Depth	Para-para	Ortho-para	Total
A_{00}	3"-2"	0.114 ± .026	0.076 ± .025	0.190 ± .028
A_0	2"-0"	0.037 ± .005	0.062 ± .007	0.100 ± .009
A_2	0"-1½"	0.0038 ± .0029	0.033 ± .016	0.036 ± .016
B_2	1½"-13"	0	0.133 ± .084	0.133 ± .084
Total		0.156 ± .026	0.303 ± .086	0.459 ± .090
Total Applied ('52-'58)		1.200	0.400	1.600

nical grade DDT (West and Campbell 1952). Apparently the ortho-para isomer disappears from the soil much less rapidly than does the para-para isomer.

Much of the DDT detected in 1958 was in the surface organic layers, but both isomers occurred in the A_2 horizon and, the ortho-para isomer, in the B_2 horizon. The greater persistence of the ortho-para isomer apparently results in gradual leaching of this isomer into the subsoil.

These data make possible estimation of the longevity of DDT in this soil if the amount landing in the ecosystem at the time of spraying is known.

Dye-card estimates (Davis and Elliott 1953) of the spray deposits made by personnel of the Forest Biology Laboratory, Fredericton, New Brunswick, and generously made available to this project, coupled with estimates from dye cards and assays of deposits made on aluminum foil sheets during spraying in Maine, all indicate that approximately 0.2 lb of DDT per acre falls on the soil in the open for each ½ lb of DDT released by the plane. The remainder is probably dispersed as small crystals in the atmosphere. The soils of the present study are a part of an ecosystem which received an estimated total deposit of 1.6 lbs of DDT between 1952 and 1958. Of this, ¾ or 1.2 lbs per acre was para-para isomer; ¼ or 0.4 lb per acre was ortho-para isomer. Approximately ¾ of the total amount of ortho-para applied was present in the soil in 1958, while about 1/10 of the total amount of para-para applied persisted. Apparently the para-para is lost quite rapidly within the year of application, while the ortho-para persists for several years. So the persistence problem, if problem it is, involves principally the ortho-para isomer.

If the rate of loss of the ortho-para isomer is linear and constant from year to year, then the amount of DDT remaining after x years could be expressed as $Y = b_0 + b_1 x$,

where Y = the amount of DDT remaining x years after spraying
b_0 = the amount landing in the ecosystem at the time of spraying
b_1 = the rate of loss of the ortho-para isomer.

If spraying were accomplished in successive years, then the amount of DDT present after x years in which n sprayings occurred would be the sum of these equations for each of the n sprayings:

$$S^n(Y) = S^n(b_0) + b_1 S^n(x)$$

For this equation we know from the data above the $S^n(Y)$, the $S^n(x)$ and we have estimates of the $S^n(b_0)$. Substituting these data into the equation for each year's deposit, the 1958 deposit of the ortho-para isomer would be expressed by:

$$
\begin{aligned}
1958 \quad Y &= 0.05 + 0 \\
1957 \quad Y &= 0.05 + 1\ b_1 \\
1956 \quad Y &= 0.05 + 2\ b_1 \\
1955 \quad Y &= 0.05 + 3\ b_1 \\
1954 \quad Y &= 0.05 + 4\ b_1 \\
1953 \quad Y &= 0.05 + 5\ b_1 \\
1952 \quad Y &= 0.10 + 6\ b_1
\end{aligned}
$$

summing: $0.303 = 0.40 + 21\ b_1$

solving: $0.097 = 21\ b_1$

$b_1 = -.005$ lb ortho-para DDT/acre/year.

This rate would mean that the ortho-para isomer deposited by a single spraying in which ½ lb/acre was released from the plane would persist for about ten years in this soil under these conditions. The work of Lichtenstein and Schultz (1959) on crop soils suggests that the rate of loss of DDT from soil is inversely proportional to the amount applied, at least in the range of 10-100 lbs/acre. If such a relationship holds for the low quantities applied to forest stands, then the rate of loss is probably higher than indicated and the 10-year estimate for the persistence of residues of a single deposit is a maximum.

The present work confirms the persistence of DDT residues in this forest soil, indicating that the ortho-para isomer is approximately 10 times as persistent as the para-para isomer and, as a result of its persistence, is leached into the subsoil.

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Intraspecific Competition as a Factor In the Natural Control of The Douglas-Fir Beetle

BY
L. H. McMULLEN
M. D. ATKINS

THE DOUGLAS-FIR BEETLE (*Dendroctonus pseudotsugae* Hopk.) causes continuous, although usually unspectacular mortality to its chief host, Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco), in the interior of British Columbia. The insect prefers weakened or recently fallen trees. When local populations become epidemic, they can usually be associated with logging or other factors which create large quantities of suitable host material. However, the general causes for the rise and fall of Douglas-fir beetle populations are not fully understood. Studies of brood mortality had indicated that a great proportion of the mortality could not be attributed to obvious factors, such as parasitism and predation, but was believed to be the result of intraspecific competition.

The effects of overcrowding on bark beetles have received little attention. Nuorteva (1954) showed that brood production of *Blastophagus pini* L. decreased greatly at high levels of competition and that the maximum number of progeny were produced at gallery densities of 60 per square meter (5.7 per sq. ft.). Knight (1958) reported that *Dendroctonus engelmanni* Hopk. produced maximum progeny when egg gallery length was between 40 and 50 inches per square foot. He found a similar, but more variable relationship to the number of entrance holes.

This paper covers the results of studies conducted near Lumby, British Columbia, in 1956 and 1957 and Lac la Hache, B. C., in 1958, to determine the role that intraspecific competition may play in brood production by the Douglas-fir beetle. Observations of caged material were made in all three years and of uncaged material in 1958.

Methods

During the early flight period in May, attack by the natural population was allowed to take place on four-foot logs until the approximate desired attack density was attained. Each log was then placed in an insect-proof cloth cage (Fig. 1). Freshly felled Douglas-fir logs were placed in each cage one to two weeks following the initial caging to absorb re-emerging parents. The logs containing the 1956 and 1958 broods were peeled and examined the following spring; those containing the 1957 brood were examined in September of that year. The bark of each log was examined in sections, each being one half the length and one quarter the circumference of the log. Records taken included the number of galleries, the length of the galleries (meas-

Contribution No. 667, Forest Biology Division, Research Branch, Department of Agriculture, Ottawa, Canada. The authors are stationed at the Forest Biology Laboratory, Victoria, British Columbia. Thanks are due R. R. Lejeune, Officer-in-Charge, and J. M. Kinghorn for their many helpful suggestions in the preparation of the manuscript. Manuscript received July 7, 1960.

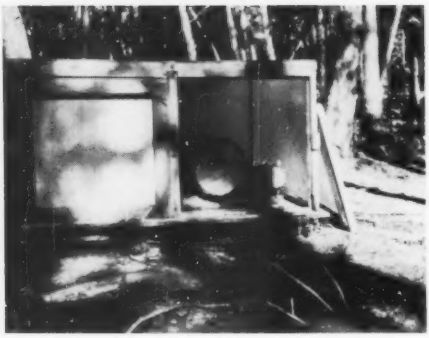

FIGURE 1. *Cages used in study.*

ured from the point where the beetle reached the wood), and the number of progeny which reached the teneral adult stage. The number of complete galleries plus one-half the number of partial galleries in each sample constituted the estimated number of galleries for the sample. All galleries, measurable at the cambial surface, were included.

Some of the young adults of the 1956 brood, and all of those of the 1958 brood emerged in the cages before the logs were examined. These were collected and recorded as they emerged and were allocated to the eight sections in each log in proportion to the number of exit holes occurring in each section at the time of examination. The number of beetles emerging per exit hole in the 1958 cages (1.65, standard deviation (SD) = 0.75) was relatively constant. Over 95 percent of the 1957 brood had reached the pupal stage at the time of examination; all living progeny were recorded as adults.

The natural population in four-foot logs was examined in 1958 at different stages of development to determine when the effects of competition take place. The samples were taken in a manner similar to that in the cage studies; data recorded included the number and length of galleries, the number of eggs, egg niches, larval mines, larvae of each instar, pupae, teneral adults, and parent adults. The number of larval mines included all those recognizable as such immediately adjacent to the side of the egg gallery, but only those originating from galleries, or portions thereof, in the sample. The number of egg niches was used to represent the number of eggs since the latter was difficult to determine in galleries examined during late stages of brood development. The number of eggs per egg niche was relatively constant (0.823, (SD) = 0.093) in data taken during early stages of brood development.

The average stage of brood development, determined from the numbers of each progeny stage present in each sample, was used as an index of maturity of the attack. The stages of brood development were grouped into three classes, representing the first and second instars, third and fourth instars, and the pupal and teneral adult stages, and are referred to hereafter as stages 1, 2, and 3, respectively.

Egg mortality was based on the difference between the number of egg niches and the number of larval mines. Similarly, larval and pupal mortality was based on the difference between the number of larval mines and the number of surviving progeny. The few young adults found dead in the samples were considered as having completed development. All densities are based on one square foot of cambial surface. Both attack density (gallery density) and egg gallery length per square foot were used as criteria of competition. Egg gallery length also was used to measure the effect of competition on the parent beetles.

Results

The study findings can be divided into two general categories: the effects of competition on parents and on progeny. Although competition is evident among the parent beetles they have the ability to leave the galleries and establish new broods in other host material.

Table 1 describes the logs and samples used in the study. The data presented graphically in Figure 2 are based on averages of measurements falling within attack density or gallery length classes, the mid-

points of which are indicated in the figure.

Effect on parent beetles. Competition for space affected the parent beetles in several ways and was reflected by the length of time parents remained in the galleries, the degree of parental mortality within the galleries, the length of galleries and the number of eggs deposited.

The length of time parents remained in their galleries was measured by the presence or absence of live beetles when the logs were examined at different stages of brood development in the 1958 field study. As illustrated in Figure 2A, the average number of parents in each gallery at stage 1 (30 to 40 days following attack) was nearly 1 at an attack density of 5 but was less than 0.1 at the higher attack densities. This difference in the number of parents present also was evident at later stages of gallery development (40 to 60 days and 60 to 80 days following attack for stages 2 and 3, respectively), but was not so pronounced since the parents tend to leave the galleries in any case after a period of time (Bedard 1950, Walters 1956). The males leave before the females (Atkins 1959) and consequently the majority of beetles remaining in the galleries are females extending the galleries and depositing eggs.

Almost 6 percent of the parents (assuming 2 parents per gallery) in the 1958 field study were found dead in the galleries. The percentage increased from early to late stages of development but was inversely related to attack density. This appears to be a reflection of the length of time that the parents remained in the galleries. At high attack densities fewer dead parents were found because they abandoned the galleries more rapidly than at low attack densities.

The average gallery length in 1958 was used to illustrate the effect of competition on gallery construction (Fig. 2B). Data from the 1956 and 1957 cage studies yielded similar results. The inverse relationship between gallery length and attack density was probably a reflection of the length of time the parents remained in the galleries. For the same reason the average length of galleries at stage 1 was shorter than at stages 2 and 3 at low attack densities, while at high densities the gallery lengths were similar at all stages. At low densities the parents were still extending galleries at stage 1.

The average gallery lengths at attack densities above 17 per square foot tended to remain the same, just over 5 inches, an indication that the parents require a period of time to feel the effect of the competition. It may, however, be related to time required for physiological changes to take place in preparation for flight (Atkins 1959, Reid 1958).

Although there was an inverse relationship between average gallery length and attack density, the total gallery length per unit area increased with attack density, but not proportionately. However, the relationship between attack density and gallery length per square foot can be satisfactorily represented by the regression $Y_e = 24.10 + 4.21\ X$ ($r = 0.8453$, $P = <0.001$). The data for this line were taken from the

TABLE 1. Log and sample data for the experimental units.

	No. trees	No. logs	D.i.b.[1] (ft.) Mean	D.i.b.[1] (ft.) Range	No. samples	Sample area (sq.ft.)	No. galleries	Galleries/sq.ft. Mean	Galleries/sq.ft. Range
Cages 1956	2	18	1.01	0.84–1.23	144	196	650	3.3	1–9
1957	2	12	0.98	0.75–1.15	96	150	760	5.1	1–10
1958	5	20	0.95	0.58–1.58	160	230	2193	9.5	3–22
Field 1958	7	22	0.88	0.60–1.16	165	229	2730	11.9	4–24
Total	16	72	0.95	0.58–1.58	565	805	6333	7.8	1–24

[1]Diameter inside bark.

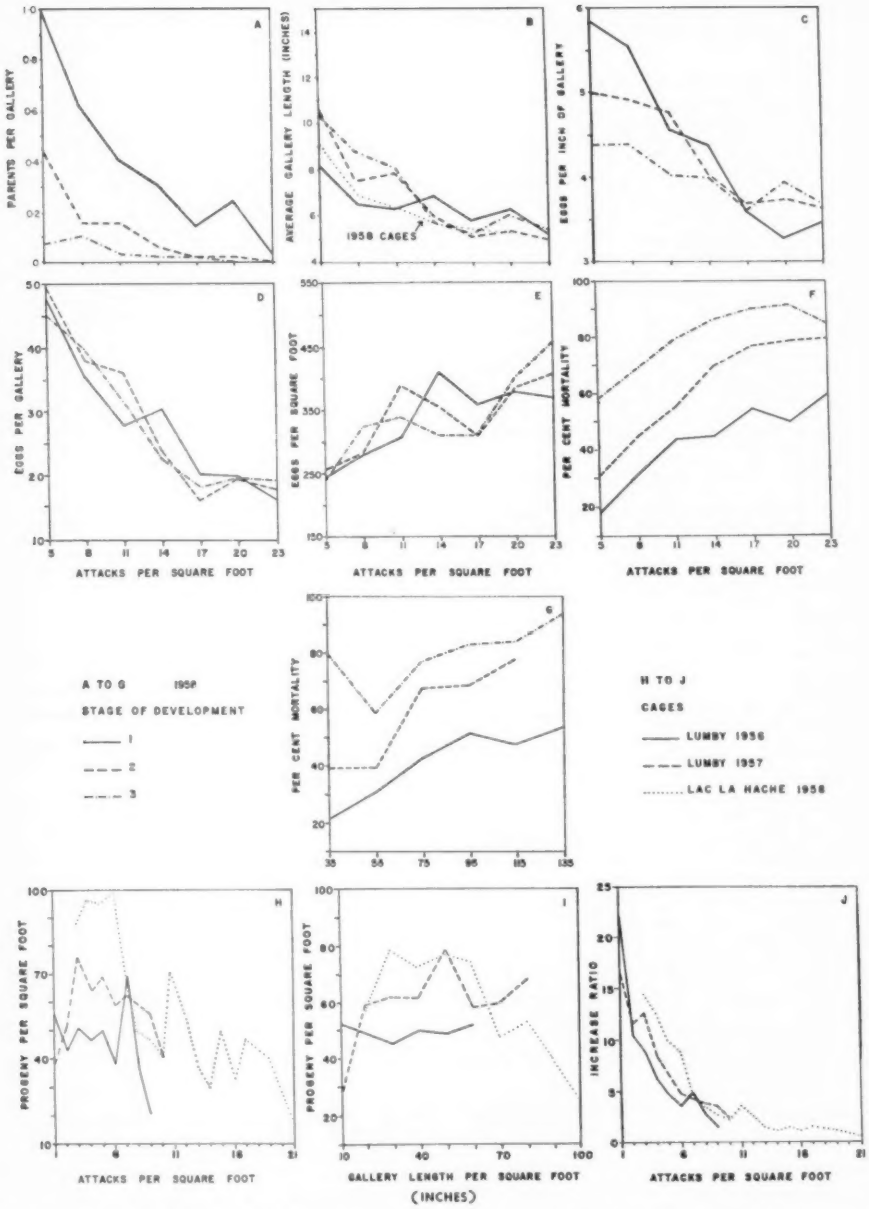

FIGURE 2. *The effect of intraspecific competition as* ***measured by attacks*** *or gallery length per square foot on: A, number of living parents per gallery;* ***B, average gallery length****; C, number of eggs deposited per inch of gallery;* ***D, number of eggs deposited per gallery****; E, number of eggs deposited per square foot; F, and G, larval and pupal mortality;* ***H, and I, progency*** *per square foot;* ***J****, increase ratio.*

1958 cage and field studies at stage 3.

Cage data for 1956 and 1957 gave steeper slopes ($b = 6.32$ and 8.27, respectively). Probably this was due to the attack densities being lower (Table 1) and the increase in total gallery length being greater over that range.

The effect on the number of eggs deposited is illustrated by the number of eggs per inch of gallery (Fig. 2C). Again there was a definite downward trend as the attack density increased. This effect is accounted for in part by the fact that there is a portion of the gallery, averaging slightly less than one inch, at the entrance which is unused; consequently, when the galleries are shorter and their density higher, there is a greater proportion of unused gallery. The rate of oviposition per inch of gallery at low attack densities was higher in samples examined at stage 1 than in those examined at stages 2 and 3. This feature can possibly be explained by slower rates of oviposition during later stages of gallery construction. However, subsequent observations to elucidate this point have shown no differences.

The total number of eggs per gallery decreased from about 50 to about 20 at attack densities of 5, and 17 to 23, respectively (Fig. 2D). This simply illustrates compounding of the effect on average gallery length and eggs per inch of gallery.

The rate of oviposition as measured by eggs per gallery and eggs per inch of gallery remained about the same at attack densities of 17 and above. This is probably a reflection of the rate of gallery construction (Fig. 2B) but is difficult to attribute to physiological changes taking place in the beetle in preparation for flight. One would anticipate that oviposition would decrease markedly at this point.

The density of eggs per square foot tended to increase with attack density, but with considerable variation (Fig. 2E), and is better expressed as a function of gallery length per square foot ($Y_e = 109.86 + 2.79X$, $r = 0.7804$, $P = <0.001$).

Effect on progeny. The effect of competition on the progeny was measured throughout brood development in the 1958 field studies and at the end of brood development in all the cage studies. Measurements included egg mortality, the number of larval mines, larval mortality and the number of progeny produced.

Egg mortality averaged 13.8 percent, varied widely, and no difference could be associated with differences in attack densities. Consequently the number of newly-hatched larvae per square foot, as measured by the number of larval mines initiated, was similar to, but at a lower level than, the number of eggs per square foot (Fig. 2E).

In Figure 2F mortality during the larval and pupal stages is considered cumulatively for the three stages of development. It followed a definite upward trend from low to high levels of competition. Mortality occurring at each stage (Table 2) indicated that the effect of competition is felt earlier at high attack densities. In fact the mortality occurring in stage 3 appears to be inversely associated with attack density because a larger proportion of the population at higher densities have died in stages 1 and 2. Similar relationships are evident when this mortality is considered by total gallery length class (Fig. 2G).

TABLE 2. Percent mortality occurring at three stages[1] of development of the Douglas-fir beetle by attack density class.

Attack density class (No./sq. ft.)	Stage 1	Stage 2	Stage 3
5	18	13	27
8	32	14	24
11	44	11	24
14	45	25	16
17	55	22	14
20	51	28	13
23	60	20	5

[1]See text (methods) for description of stages.

The density of progeny produced in the cage studies is shown by attack density class in Figure 2H. Although there was considerable variation there was a definite trend toward lower numbers of progeny at higher attack densities. The maximum number of progeny was produced when attack density was about 4 to 8 per square foot. A similar relationship occurred when progeny production was plotted against total gallery length (Fig. 2I), the maximum number of progeny being produced between total gallery length classes of 30 to 60 inches per square foot. Similar results were obtained from the 1958 field studies except that the peaks were shifted towards higher levels of attack density, apparently because the effects of competition were not complete at the time the samples were taken.

The relationship between attack density and progeny production was more vividly evident when plotted as an increase ratio (Fig. 2J). The increase ratio assumed two parents per gallery and was calculated as the number of progeny divided by the number of parents. There was a marked decrease with increasing attack density but with a levelling-off to an increase ratio of approximately 1 at attack densities of 13 and above.

Discussion

The effects of overcrowding were evident throughout the development of the insect under the bark. The total effect up to the teneral adult stage, as represented by the numbers of progeny produced at various attack densities (Fig. 2I) is the result of effects on different aspects of the activity of the beetles (both parents and progeny) during the establishment and development of the brood. Figure 2J represents the total effect in terms of an increase ratio (or in reduction from potential).

There are several factors which must be kept in mind in interpreting the data which are presented here. One of the most important is, as mentioned previously, that the parents attack more than once. Only the brood resulting from the initial attack is considered here. It was shown that those parents which were subjected to high levels of competition left their galleries more rapidly than did those subjected to low levels. Those parents leaving the galleries are presumably capable of producing additional broods. This feature tends to offset some of the effects of competition as illustrated here. However, it would not be unreasonable to assume that the effort required by the beetles to leave their galleries and establish new ones would create a considerable drain on their vitality. Moreover, when they leave the galleries they may be exposed to adverse environmental factors not encountered under the bark.

It is of considerable significance in the population dynamics of the insect that the number of progeny is reduced at high attack densities. During 1956, 1957, and 1958, the general population of the Douglas-fir beetle was increasing following a sharp reduction during the winter of 1955-56 (McMullen 1956). The increasing attack densities obtained in this study in successive years is possibly a reflection of the increasing population. If attack density is a reflection of population levels, as the population increases the attack density will increase with a consequent reduction in progeny production. The effect of competition thus acts as a regulating feature to keep the population in check.

The same reasoning could explain why the insect frequently attacks living trees in logging operations. When there is an abundance of suitable host material, the population can build up locally to high levels at low attack densities. As logging continues and the insect continues to breed in slash the population increases to the point where intraspecific competition in the slash becomes regulatory. Providing that logging is maintained at a constant level in adjacent areas year after year the beetles should attack their preferred host material, the slash. But as soon as there is fluctuation in the logging, and insufficient (preferred slash

host material) is available for the attacking beetles, the overflow will go into standing timber.

Mortality factors other than competition could be greatly influenced by the effects of competition. A given number of predators or parasites could have a greater relative effect on the population when the numbers of progeny are low, although the search problems of the enemies would be increased. In addition, the percent mortality of overwintering beetles is higher when fewer individuals are present (McMullen, unpublished data).

Attack densities of less than 3 per square foot are seldom encountered in the field because the insect tends to select and congregate in suitable host material. The important effects are felt at the higher attack densities, i.e. above 4. As outlined in the previous paragraph, parasites and predators could exert a greater proportional effect on low numbers of progeny. This would be particularly true after these natural control agents have had a chance to increase in situations where their host population was increasing. Such climactic situations, which are possibly quite common, could explain a sudden decline or severe reduction of populations.

Summary

Studies of the effects of intraspecific competition on the Douglas-fir beetle in logs are described. As crowding increased the parents abandoned the egg galleries more rapidly, the egg galleries were shorter, fewer eggs were laid, and mortality during the larval and pupal stages was higher. The maximum number of adults was produced at attack densities of 4 to 8 per square foot and at total gallery lengths of 30 to 60 inches per square foot. The increase in progeny was highest at the lowest attack density and dropped to a ratio of 1:1 at attack densities of 13 to 17 per square foot. The implications of the net effect on populations are discussed.

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Maturation of Douglas-Fir Seed— A Biochemical Study

BY
J. H. REDISKE

WITH THE INCREASING EMPHASIS on immediate regeneration of cutover lands, more attention is being directed to the consistent production of large quantities of high quality forest tree seed. Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco), as is common with most conifers, produces seed in cycles. The intervals of time between good seed years vary, but are usually long enough that the demand for seed exceeds the supply.

Many possibilities for obtaining maximum use of the available cone crop depend upon a knowledge of the ripening process so that the level of seed maturity can be determined. Thus, cones could be picked as soon as the seed matures to make full use of the season. Furthermore, by picking immature cones and then ripening artificially, as suggested by Silen (1958), the maturation process could be followed and the seed extracted for proper storage when mature. Knowledge of when seed is mature would make possible (1) the maximum extension of the season for cone collection. (2) the processing of only mature seed, and (3) the storage of seed under optimum conditions when mature.

Over the years several measures of maturity have been suggested. Specific gravity has been shown to be a reliable index of maturity for some species of pine (Schubert 1955, Maki 1940). Cram and Worden (1957) indicated that moisture and specific gravity are indices of cone and seed maturity for white spruce. Moisture content and specific gravity are manifestations of the biochemical maturation going on within the cone and seed. The most important biochemical process is the change from mobile to storage forms of food within the embryo and endosperm itself. Little is known of the biochemical maturation of conifer seeds, although much has been written about this process in plants where the seed is an important item of food (Crocker and Barton 1953).

It is the purpose of this paper to report the results of a study to determine the important biochemical constituents of Douglas-fir seed and to correlate the concentration of these constituents with maturity as determined by germination when the seeds were ripened naturally and artificially.

Materials and Methods

Two 20- to 30-year old Douglas-fir trees about a mile apart on the Clemons Tree Farm near Montesano in southwestern Washington, were selected for this study. The data presented herein are from one of these trees. Results from the other tree were similar in all respects except for a few days' difference in phenology. Cone samples were picked in a random manner from each tree on August 2, August 16, August 30, and September 19, 1957. The cones for each picking date were divided into two lots. One lot was dried and the seed extracted as soon as possible (about two weeks) after picking. This seed was

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placed in cold storage at −19° C and sampled at four-week intervals. The other lot of cones from each picking date was stored in burlap sacks in the shade. After each four-week interval 150 cones were removed for seed extraction. The seed was dewinged by hand and cleaned with care to avoid any fractionation of filled from empty seed. Seed from both lots were then checked for germination and the planned chemical analysis performed.

Germination tests were conducted using five samples of 100 seeds each. This number of seed was found to give a germination percent within five of the mean. Each sample was placed in a square, plastic petri dish and sufficient moist Sponge Rok[1] added to cover the seeds. After replacing lids the dishes were set in the refrigerator to stratify for 14 days at 40° C; afterwards they were placed in a germinator at 24° C. At seven-day intervals, the dishes were removed, and germinated seeds picked out and counted; then moisture was added to the remaining ungerminated seeds in the Sponge Rok, and the dishes replaced in the germinator. This was repeated until no further germinates were obtained. Most lots had completed germination within 14 days; a few required 21 days.

Seeds were ground in a Wiley mill to 20-mesh fineness. Crude fat, iodine number, reducing sugars, non-reducing sugars, starch, soluble nitrogen, and protein nitrogen analyses were conducted. For the crude fat determination, duplicate, one-gram samples were placed in an alundum thimble and extracted for eight hours in a Soxhlet apparatus with 50 ml of petroleum ether. With the extraction completed, the petroleum ether was removed by evaporation and the crude fat weighed. The iodine absorption number of the fat was determined by the Hanus method (Horwitz 1955) using all of the fat from the above extraction.

[1]Paramount Perlite Co., Paramount, California.

The extraction for carbohydrates and nitrogen-containing compounds was carried out with a Soxhlet extractor using duplicate one-gram samples (Loomis and Shull 1937) The ground seed was extracted for two hours with 50 ml of 75 percent alcohol. This was replaced with an additional 50 ml for a remaining five-hour period. The residue was set aside for starch and protein nitrogen analysis. The extract was analyzed for reducing and non-reducing sugars and soluble nitrogen compounds. Alcohol was removed from 50 ml of this extract by vacuum distillation and the residue was quantitatively transferred to a 100 ml volumetric flask and made up to volume with water after precipitation with saturated lead acetate solution.

The solution was filtered through a dry filter paper and the reducing sugar content determined on one ml of the solution by the method of Hagedorn and Jensen as described in Hawk, Oser and Summerson (1937). Non-reducing sugars were determined by the same method after the addition of three drops of a 1-percent solution of invertase to one ml of the non-alcoholic extract made slightly acid to methyl red with dilute acetic acid. Results were expressed as milligrams of sugar per gram of dry seed.

The soluble nitrogen determination was carried out on 10 ml of the alcoholic extract. This was added to a micro-Kjeldahl flask with one drop of concentrated sulfuric acid and boiled until the alcohol was evaporated. A micro-Kjeldahl determination was made on the residue according to the technique of Pepkowitz and Shive (1942) and the results were expressed as micrograms of nitrogen per gram of dry seed.

Starch and protein nitrogen determinations were conducted on the residue from the above alcoholic extraction. Starch was determined on 0.1 g of residue soaked for 24 hours in 20 ml of distilled water. The sample was filtered and washed on the filter paper with 100 ml of distilled water,

the filtrate discarded, and the residue washed back into an Erlenmeyer flask with 25 ml of water. Then the sample was refluxed with 2.4 ml of concentrated hydrochloric acid for 2.5 hours. After cooling and filtering, the filtrate was neutralized with sodium hydroxide to pH 5. using methyl red as an indicator, and made up to 100 ml. A 1-ml aliquot was removed and analyzed according to the Hagedorn-Jensen procedure. The reducing sugar value obtained was multiplied by a factor of 0.90 and expressed as milligrams of starch per gram of dry seed (Horwitz 1955).

Protein nitrogen was determined on a 30-mg sample of the residue. This was analyzed by the Kjeldahl technique following the method of Pepkowitz and Shive (1942). Results were expressed as milligrams of nitrogen per gram of dry seed. Chemical analyses were conducted in duplicate to agree within 10 percent. All data were examined by standard technique for statistical analyses.

Results

Germination. Germination tests were conducted at each sampling time to measure the level of maturation and seed quality. The germination percentages of the seed obtained from cones of two picking dates, August 16 and August 30, are plotted in Figure 1. Seed extracted August 30 from cones picked on August 16, gave an average germination of 13 percent. When this extracted seed was placed in storage, the germination percentage continued to decrease until eight weeks later when the average value was 2 percent. With the same lot of cones, if the seed were allowed to remain in the cone in sacks stored in the shade, the germination percentage increased from the 13 percent to 30 percent in four weeks, and almost to 40 percent within eight weeks. Thus it was apparent that this seed was immature when picked, but by allowing the seed to remain in the cone, maturation continued.

Seed extracted within two weeks after picking on August 30 had an average germination of 33 percent. These seed tended to increase slightly in germination after extraction and cold storage, differing in this respect from seed picked two weeks earlier. Since the August 30 seed represented the maximum germination percent, it was considered mature.

Somewhat different results were obtained when seed from the August 30 lot were allowed to remain in the cones in shaded sack storage. The germination at corresponding times was found to be significantly lower than that of seed extracted immediately and placed in cold storage. Thus. it was apparent that continued storage of mature seed in the cones can prove harmful. Higher germination percentages were obtained when mature seed were extracted immediately after maturation and stored at −19°C.

In general, seed from cones picked August 2 were immature. There was a rapid loss in germination, and little ripening was obtained by shaded sack storage. The cones picked September 19 were similar to those picked August 30 in that the seed had a uniformly higher germination percentage. There was less reduction in germination associated with storage in the cone with the September 19 picking, apparently because the cones at this stage were quite dry.

Reducing sugars. Figures 2B and C represent the reducing sugar content of the same seed lots at the same sampling dates as the germination percentages in Figure 1. Seed from cones picked August 16 had a relatively high initial reducing sugar content of 22 mg per g. Four weeks later this dropped to 17 mg per g with seed extracted and stored at −19° C. With seed that were allowed to remain in the cone, the reducing sugar content continued to drop below 10 mg per g; this was synchronized with the rise in germination shown in Figure 1.

With cones picked August 30, the first

analyses were conducted on September 6. A reducing sugar content of 13 mg per g was found. This remained fairly consistent for seed which were removed from the cones after picking and stored at −19° C. However, reducing sugars decreased to 7 mg per g for seed in shaded sack storage in the cone.

The initial reducing sugar contents of four lots of cones are represented in Figure 2A by picking date. These data represent the first analysis obtained from each lot. There was a two week delay between picking and sampling due to cone-drying time, seed extraction and sample preparation. Cones picked August 2 had a reducing sugar content of 27 mg per g. The seed from these cones did not ripen in shaded sack storage, and produced low quality seed. With cones picked August 16,

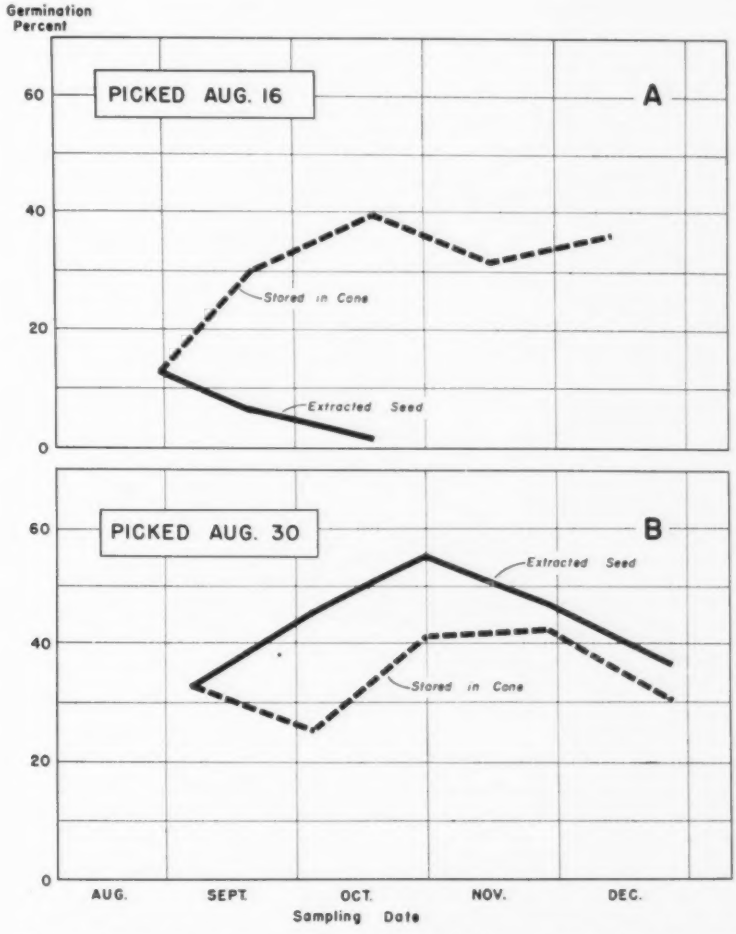

FIGURE 1. *The germination of Douglas-fir seed when extracted from the cone immediately after picking and stored in the cone for various times. A. Cones picked just before seed maturity. B. Cones picked just after seed maturation.*

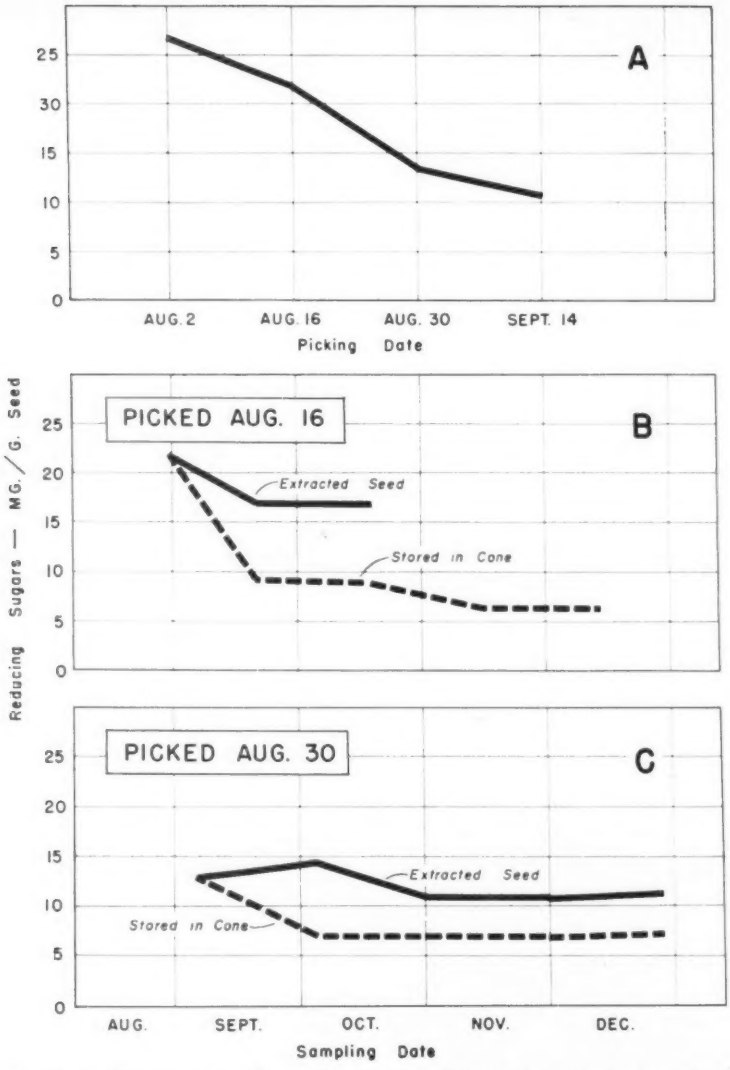

FIGURE 2. *Concentration of reducing sugar in Douglas-fir seed. A. At each of 4 picking dates. B. Sampled at successive dates after picking just before seed maturity on August 16, or, C. Just after seed maturation on August 30.*

the reducing sugar content had dropped to 22 mg per g. These cones were successfully ripened in shaded sack storage (Fig. 1). However, seed extracted immediately after picking and stored at −19° C resulted in low germination. Seed picked August 30 were mature when picked and had a reducing sugar content of 13 mg per g. Continued shaded sack storage in the cone resulted in lower seed quality. Seed picked September 19 had an initial reducing sugar content of 11 mg per g.

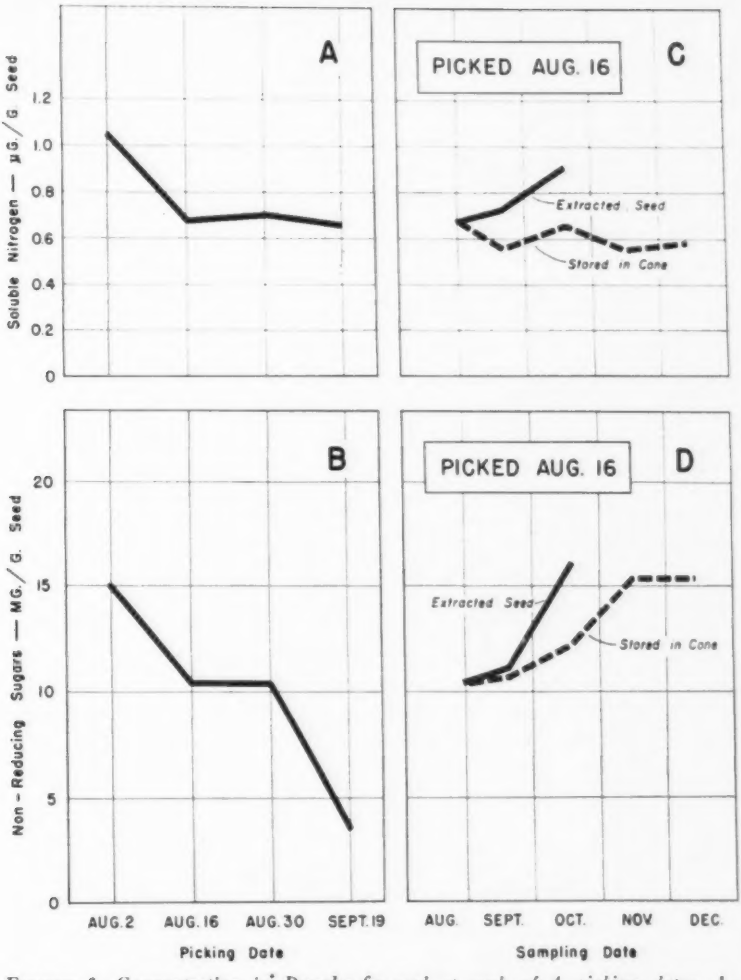

FIGURE 3. *Concentration in Douglas-fir seed at each of 4 picking dates. A. Soluble nitrogen, B. Non-reducing sugars. Concentrations in seed picked on August 16 and sampled at successive dates for C. Soluble nitrogen, and D. Non-reducing sugar.*

The germination picture was similar to that for seed picked on August 30 except that storage in shaded sacks was not harmful. Thus, it was apparent that the reducing sugar content of the seed decreased as the seed matured.

Non-reducing sugars. If cones were allowed to remain on the tree and ripen naturally, the non-reducing sugar content of the seed decreased as the cones matured (Figure 3B). This is the same trend as for reducing sugars. The non-reducing sugar content ranged from a high of 15 mg per g for cones from the initial collection on August 2 to 3.5 mg per g for cones from the final collection of September 19.

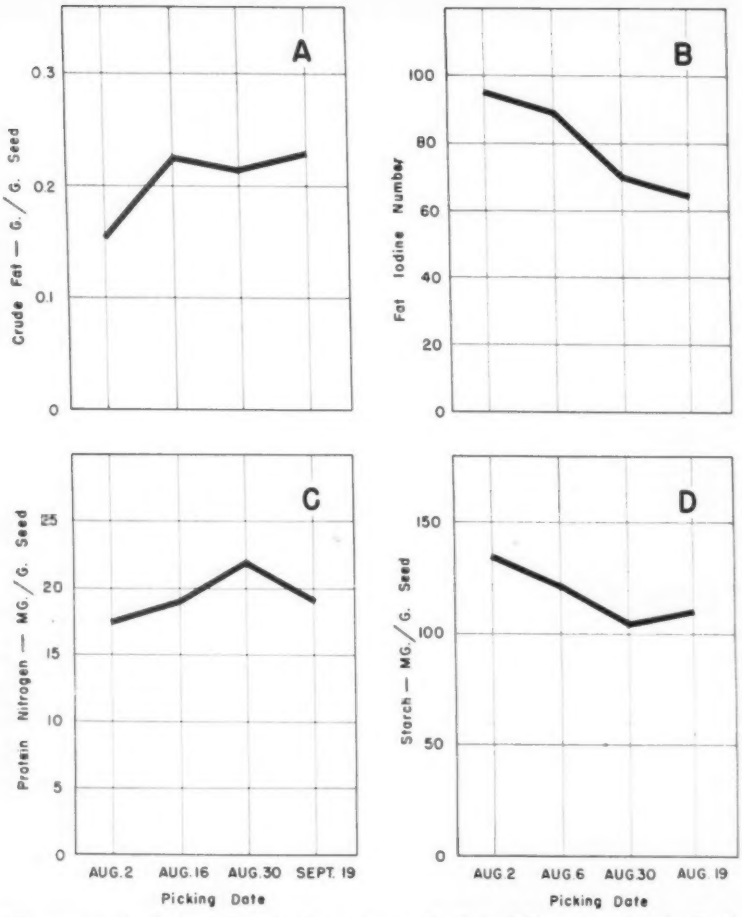

FIGURE 4. *Analysis of Douglas-fir seed at each of 4 picking dates for A. Crude fat, B. Fat iodine number, C. Protein nitrogen, and D. Starch.*

Once the cones were picked however, the non-reducing sugar content tended to increase over the initial concentration. This is evidenced in Figure 3D, which presents the data on non-reducing sugar concentrations from seed picked on August 16. Even when cones were picked fully mature on September 19, there was a slight increase in non-reducing sugar content over the initial 3.5 mg per g.

Starch. The starch concentrations of seed harvested at four picking dates are plotted in Figure 4D. The concentration for immature seed on August 2 was about 13 percent and dropped to 10 or 11 percent with mature seed. Thus, starch was found to be an important food storage form percentage-wise in Douglas-fir seed, but tended to decrease as maturation progressed.

Protein nitrogen. Protein nitrogen concentration of Douglas-fir seed from four picking dates is represented in Figure 4C. Like starch, the concentration of protein nitro-

gen proved fairly stable during the period of maturation. The crude protein concentration, estimated as nitrogen × 6.25 (Loomis and Shull 1937), amounted to about 11 percent for the August 2 picking date. This crude protein rose to a concentration of 14 percent for the August 30 picking date. Thus, crude protein, which averaged 12 percent for the season, proved an important storage form that was present in about the same concentration as starch. Furthermore, there seemed to be a reciprocal relationship between protein and starch.

Soluble nitrogen. Soluble nitrogen (in 75 percent alcohol) includes most forms of nitrogen other than colloidal or protein nitrogen, such as inorganic nitrogen and amino acids. The soluble nitrogen content was generally low in seed and decreased with the process of natural maturation (Figure 3A). When cones were picked early (August 16) and placed in shaded sack storage, soluble nitrogen concentration changed little during the critical stages of the maturation processes (Figure 3B). However, seeds that were removed immediately after picking and placed in storage at −19° C, showed a slight increase in soluble nitrogen concentration.

Crude fat. The crude fat concentration of Douglas-fir seed at four picking dates is presented in Figure 4A. Crude fat content was lowest, 15 percent, for the August 2 picking date when the seed was immature. Within two weeks, crude fat had increased to about 22 percent and the concentration stabilized for the remainder of the maturation process. Crude fat thus represents the greatest proportion of all storage forms in Douglas-fir seed. Figure 4B represents the iodine number of the crude fat extracted from the seed. As the maturation process advanced, the iodine number dropped from 95 with immature seed to 65 with fully mature seed. This represented a decrease in unsaturated bonds of the fatty acids generally signifying an increased melting point of the crude fat with maturation of seed.

Discussion

Silen (1958) has shown that immature cones could be ripened artificially by damp storage between layers of peat moss. He was able to produce seed with about 30 percent germination when picked on August 1. Immature cones can be ripened also by storage in the sack out of doors in the shade. The present study has shown that seed from cones picked on August 16 were not mature. If the seed was extracted immediately and stored at −19° C, the germination percentage dropped rapidly. However, if the seed was left in the cones in sacks stored in the shade, the germination percentage increased rapidly for the next eight weeks. It is anticipated that with improved techniques of storage the cone picking season might be extended by artificial ripening even further and still produce high quality seed.

Adverse effects on seed quality were noted if seed remained too long in the cones, especially those with high moisture content. This was apparent with the August 30 picking date. Here, seed left in the cones in shaded sack storage showed consistently lower germination than seed removed promptly after cone picking. There apparently is a time in the storage of cones when maturation is complete, and in order to maintain good quality the seed should be extracted and placed under the proper storage conditions. This is generally considered to be about −18° C and 5 to 10 percent moisture content in sealed containers (Barton 1954, and Allen 1957).

If high quality seed is to be obtained from immature cones artificially ripened, it is necessary to know the stage of maturation when the cones are picked as well as when the seed reaches maturity. The reducing sugar content has been shown to decrease during the cone ripening season in phase with increasing degree of maturation. Likewise when cones contain-

ing seeds in an immature stage are picked and the seed allowed to ripen in the cones, the reducing sugar content follows the maturation process. Thus, based on the work presented herein. Douglas-fir seed is fully mature when the reducing sugar concentration has decreased to 13 mg or less per g. Likewise seed can be artificially ripened by shaded sack storage when the initial reducing sugar concentration has decreased to 22 mg or less per g.

Even though seed may be successfully ripened artificially, there are factors of degradation which tend to reduce seed quality. These factors do not necessarily affect the reducing sugar values but may be related to other indexes. That factors of degradation are present is apparent from a comparison of the data of Figures 1A and 2B. When cones were picked August 16 and the seed extracted, the reducing sugar content dropped from 22 to 17 mg per g but germination also dropped from 13 to 6 and finally to 2 percent. But when seed from the same collection were allowed to ripen in the cone in shaded sack storage, germination increased from 13 to over 30 percent and the reducing sugar content decreased from 22 to 9 and then to 6.5 mg per g. Degradation likewise occurred in cones picked August 30. However, in this case the reduced seed quality resulted from leaving mature seed in cones of high moisture content. The highest quality seed was produced when mature cones were processed at picking time.

The present study does bring out that artificial ripening of cones involves a complex of factors, some of which may serve as indicators of maturation and others of degradation. The factors in these two classes may not be interrelated to the extent of having an effect on each other, but certainly the sum of the effect of the factors is represented in the quality of the seed and the germination potential. This is not so apparent with cones ripened on the tree. There is less opportunity for favoring the factors of degradation under conditions of tree ripening than under conditions of artificial ripening. Thus, the reducing sugar content of freshly picked cones is representative of the stage of maturation of the seed.

Suggestions have been made concerning possible factors of degradation indicative of a reduction in pine seed germination. Kaloyereas (1958) has shown a relationship between increase in seed fat rancidity and loss of seed viability. He found that coating seeds with an anti-oxidant prolonged seed viability. Mirov (1944) suggests a relationship between linolenic acid and viability during storage. These factors deal with the fat content of the seed. Since fat is the principal food storage form, it is logical to assume that some indicators of degradation will be associated with this fraction. Studies concerning Douglas-fir seed degradation now are under way.

Summary

1. Cones were collected from two Douglas-fir trees in Southwestern Washington on August 2, 16 and 30, and September 19, 1957. The seed from half of the cones from each picking date were extracted within two weeks, the remainder of the cones were placed in shaded sack storage out of doors. Both lots were sampled every four weeks for 16 weeks.
2. Cones picked on August 16 were immature. The germination percentage decreased rapidly when seed were extracted from cones immediately after picking. However, if these immature cones were placed in shaded sack storage, maturation continued, and good quality seed was produced.
3. Cones picked on August 30 were mature. Immediate extraction from the cone produced good-quality seed. However, if seed were allowed to remain in these cones in shaded sack storage, the germination was significantly reduced.
4. The reducing sugar content of Douglas-fir seed decreased as the seed ma-

tured. It was found that seed with an initial reducing sugar concentration of 22 mg per g were immature, but could be ripened artificially. Seed containing 13 mg per g of reducing sugar were mature. Reducing sugar content of Douglas-fir seed was found to be a good biochemical indicator of maturity.

5. The non-reducing sugar concentration decreased from a high of 15 mg per g with immature seed to a low of 3.5 mg per g with mature seed when ripened on the tree. However, when ripened artificially the non-reducing sugar concentration increased from the picking date.
6. The differences of starch, soluble nitrogen and protein nitrogen concentrations between immature and mature seeds were relatively minor with high concentrations of 13 percent, 1 μg per g and 22 mg per g, respectively.
7. The crude fat concentration increased from 16 percent when immature to 23 percent when mature. The iodine number of this fat decreased from 95 to 65 during the same interval.

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Salt Secretion by Tamarix pentandra *Pall.*

BY
JOHN P. DECKER

FIVE-STAMEN TAMARISK (*Tamarix pentandra* Pall.) is an abundant phreatophyte in the southwestern United States. Typically a large shrub, it often forms extensive and nearly impenetrable stands along banks and flood plains of streams. It is commonly known as saltcedar because leaves are minute and scale-like and are often coated with a salty white bloom. During periods of high humidity, twigs often become laden with droplets of salty fluid. Gatewood *et al.* (1950) analyzed fluid shaken from shrubs along the Gila River and found it to contain up to 41,000 ppm total solids, most of which was NaCl.

This paper reports a study of the origin of salty bloom on tamarisk twigs. Two kinds of twigs were studied—typical growth with scale-like leaves (usually about .5 x 1 mm), and sprout growth with leaves often about 3 x 7 mm. Because sprout leaves were larger and more easily handled, most initial observations were made on them.

Bloom on sprout and typical foliage of shrubs in the field and on plants grown from cuttings in a greenhouse upon examination with a 10× hand lens was found to consist of whisker-like columns (Fig. 1) and various crystals. Whiskers ranged in shape from nearly regular cylindric to irregular, contorted, and sometimes branched. They appeared white, opaque, and minutely granular. Crystals varied from partly opaque irregular masses to transparent glittering cubes (Fig. 2).

A large leaf (about 3 x 6 mm) was examined dry with a 100× microscope. The bloom consisted mostly of whiskers, with only a few crystals. A drop of distilled water was inserted under the leaf so that the leaf was partly floating on water but the upper surface remained dry. Whiskers and crystals began to dissolve almost immediately. Within 5 minutes all were replaced by glistening spherical droplets. Excess water was withdrawn from under the leaf with blotting paper. After a few minutes the leaf was completely dry again. All whiskers were gone and only glittering cuboid crystals remained. The experiment was repeated several times with this leaf and several others with virtually identical results. No whisker was ever seen to reform after dissolving, whereas cuboid crystals reformed repeatedly. These observations indicated that salty white bloom on tamarisk foliage originates as whiskers later recrystallize into new shapes.

Origin of Briny Fluid

Gatewood *et al.* (1950) made the reasonable suggestion, based on field observations, that the briny fluid on tamarisk shrubs was guttated, that is, forced out by internal hydraulic pressure created by roots. The following observations and experiments indicate, however, that deliquescence of salt crystals by atmospheric moisture was mainly involved.

Melting of whiskers and crystals, on the surface of a leaf either afloat on a drop or simply exposed to high humidity, was observed repeatedly under a microscope. The

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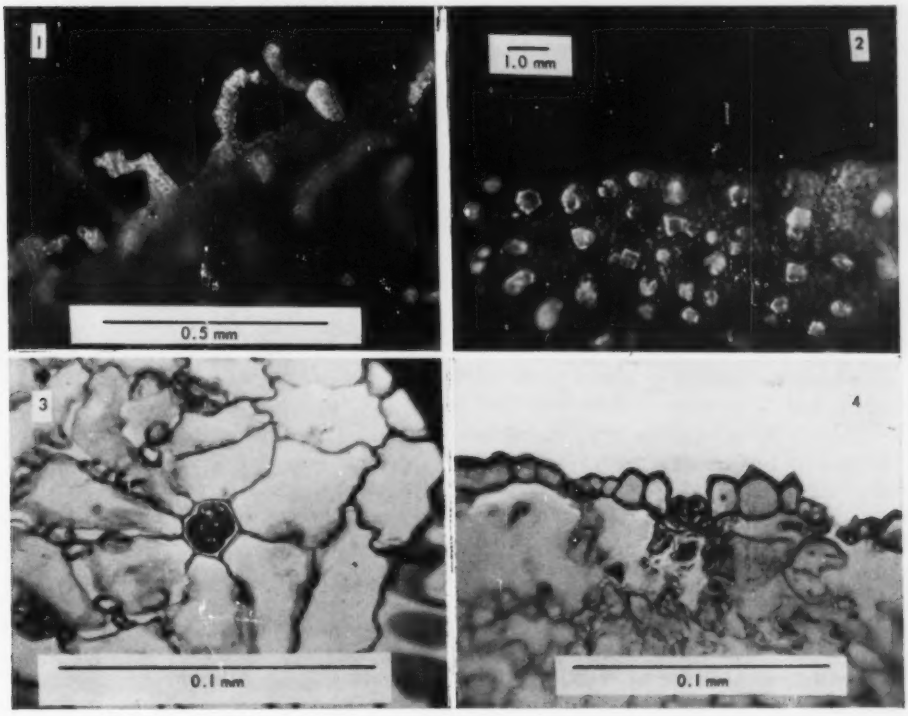
Permanent slides used in this study were prepared by W. S. Phillips and R. L. Hall, University of Arizona, Tucson. Manuscript received July 20, 1960.

base of a whisker or stalk was always last to dissolve. If water responsible for dissolving the bloom were fluid water from the leaf, melting would begin at the base. Therefore, the water evidently came from an external source.

In the second series of experiments twigs were pretreated and then exposed to high humidity. High humidity was generated by covering a small potted tamarisk plant with an inverted glass jar. Study materials and pretreatments were as follows: (1) normal twigs, intact, (2) normal twigs, freshly severed. (3) normal twigs, severed and left to dry overnight on a table top, (4) intact twigs washed nearly free of bloom, and (5) severed twigs washed nearly free of bloom.

Several twigs were suspended among intact twigs; the jar was lowered into place; and the assembly was spotlighted from one side in a dimly lighted room. Within 5 minutes many glistening droplets began to appear on all fresh twigs that had not been washed. Only an occasional droplet appeared on those that had been washed. Within another 5 minutes many droplets appeared on the twigs that had dried overnight. The jar was removed and was replaced again after droplets had dried and disappeared. Droplets began to reappear as before, but this time there was less lag



FIGURES 1–4. *Retouched photomicrographs of: 1. Upper surface of tamarisk sprout leaf with salt columns. 2. Upper surface of sprout leaf showing incrustation of cuboid crystals. 3. Flatwise section through upper epidermis of tamarisk sprout leaf showing dense 2-celled salt gland surrounded by rosette of epidermal cells. 4. Longitudinal section of scale leaf showing salt gland in epidermal pit.*

between fresh twigs and those dried overnight. Formation of droplets was clearly dependent on humidity and on presence of salty bloom. Behavior of severed twigs showed droplet formation to be clearly independent of root pressure. Thus, the briny fluid often found on twigs and foliage of tamarisk shrubs in the field probably results from deliquescence of previously secreted salty bloom rather than from current guttation.

This conclusion is supported further by the absence of easily demonstrated root pressure in this species. If the copious production of briny fluid resulted from guttation and therefore from root pressure, tamarisk branches should bleed freely when cut. They do not. Cut surfaces of branch stumps were examined repeatedly throughout the previous experiments and have been examined many other times in field and greenhouse. No evidence of root pressure (wetting of stump surface) has been observed.

Origin of Salt Whiskers

A fresh sprout leaf was mounted dry on a microscope slide and examined at 100× by reflected light. Several short whiskers were teased off with needles. Each appeared to arise from a small pit or gland that was surrounded by a rosette of epidermal cells.

Another short whisker was examined as the leaf surface was flooded with distilled water. As the last traces of the base melted away, a gland was revealed directly beneath. The preparation was then allowed to dry. As the water dried down to a very thin glistening film, surface configuration became sharply outlined. The gland was dome-shaped and was in a small pit. The procedure and observations were repeated with several other columns.

Salt glands have been observed previously in tamarisk (McClintock 1951) and are well known in many other halophytes (Helder 1956). No previous report of whisker-like salt columns has been found.

Anatomy of Salt Glands

Short pieces of twigs were cut from shrubs along the Salt River near Granite Reef Dam, Arizona, and were put immediately into killing and fixing solution (formalin-acetic acid-alcohol). They were dehydrated in an alcohol series, transferred to tertiary butyl alcohol, infiltrated with paraffin, and imbedded in paraffin. Serial sections were stained with safranin, fast green and orange G.

Figure 3 is a flatwise section through the upper epidermis of a sprout leaf that includes a cross section of a salt gland. More than 50 such glands were examined. All appeared essentially similar: two-celled, densely packed with granular material, non-vacuolate, and surrounded by a rosette of epidermal cells.

Figure 4 is a longitudinal section of a scale leaf that shows a salt gland in vertical section. More than 100 such sections of glands in scale and sprout leaves were examined. Exterior walls of glands were always dome-shaped or nearly so. Glandular cells always appeared non-vacuolate. Arrangement of granular material was variable, but fingerlike structures similar to those visible in Figure 4 appeared in about 50 percent of the glands examined. Mesophyll tissue immediately beneath a gland was always conspicuously more compact than adjacent tissue. A drawing of a salt gland of *Spartina* by Skelding and Winterbotham (reproduced by Helder 1956) shows that gland to resemble generally a gland of tamarisk but to differ from it in cellular details.

Physiology of Salt Secretion

According to Helder (1956) the mechanism of secretion by halophytic salt glands is unknown. Lack of information about this biological desalting device is unfortunate in view of the current worldwide interest in practical techniques for desalting saline water.

The present study yielded no information about the secretory mechanism itself,

that is, about how salt is secreted onto the external surface of a gland. However, information was obtained about the next step, accretion, or the development of secreted salt into whiskers.

Suggested Mechanism of Whisker Development

Actual enlargement of a whisker was not observed, but the mechanism of enlargement can be inferred from the texture and shape of whiskers. Accretion was probably by repeated minute additions at the base of a whisker. Additions were irregular and were probably made at several places on the external surface of the gland.

The finely granular texture of a whisker indicates that only a minute quantity of salt solution was present at any one time. A larger quantity would have induced formation of coarser crystals. Dependence of texture on amount of solution was indicated by the formation of coarser crystals whenever a whisker redried after deliquescing even slightly. Dependence of crystal size on amount of solution can be observed also with ordinary salt solution drying on a microscope slide; minute puddles of solution give rise to feathery dendrites only, whereas coarse pyramidal crystals form in larger pools of solution.

The roughly cylindric shape of a whisker indicates that additions were basal. If salt accreted by soaking into a whisker before drying, radial increment as well as coarser crystals could be expected. Irregular shape of a whisker indicated that secretion was irregular and perhaps from several places on the external surface of a gland.

Brenner (1958) observed and photographed salt whiskers that had developed on the outside of a cellophane bag filled with NaCl solution and suspended in air. Development of whiskers in this simple physical system suggests that no complex biological mechanism need be proposed to explain development of whiskers from salt secreted by tamarisk foliage.

Problems for Further Study

Several other questions now arise: What is the minimum internal salt concentration that will set the gland in operation? How is this concentration attained in a gland? Is the internal functioning of a tamarisk salt gland somewhat similar to that of salt concentrating glands of gooney birds (Frings *et al.* 1958)? Is salt secretion related to transpiration? That is, does salt move up in the transpiration stream and somehow arrive at the salt glands rather than concentrating at the evaporating surfaces of the mesophyll?

Summary

Foliage of tamarisk is often covered with a bloom of salt that is secreted by salt glands imbedded in epidermal pits. Glands are dome-shaped and consist of at least two cells which are non-vacuolate and densely filled with granular material. Salt appears initially as minutely granular, whisker-like columns arising from the glands. Whiskers often deliquesce and recrystallize as large cubes.

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Rot Entrance Through Dead Branches of Southern Hardwoods

BY
E. RICHARD TOOLE

THE FUNGI THAT CAUSE heart rot in southern hardwoods most frequently enter trees through basal wounds made by fire or in logging, but they also enter through bark breaks above the zone exposed to these hazards. The breakage caused by falling trees, ice, snow, or wind is generally recognized as providing courts of infection to the upper bole. This paper deals with the kind and amount of rot traceable to a less spectacular source—the stubs and wounds caused by the normal death of limbs.

The literature contains little on this subject for the southern hardwood types, but Hepting *et al.* (1940) included branch stubs in their evaluation of external features correlated with top rot in Appalachian oaks. Because of the great variation in amount of rot associated with external indicators, they hesitated to correlate the rate of linear spread with specific features. Instead they set up risk classes based on number, condition, and size of stubs.

Genaux and Kuenzel (1939), working in oak-hickory stands in Iowa, found that 10 percent of their sample trees had decayed branch stubs; average length of heart rot originating from these stubs was 19 inches. Other literature on heart rots in living trees is reviewed by Wagener and Davidson (1954).

The present investigation determined the incidence and extent of rot associated with dead branches, branch wounds, and branch scars of different sizes and at different times after the death of the branch. An attempt was made to identify the important heart-rot fungi concerned. All of the more important southern hardwood timber species were included.

Field Procedure

Sixteen study areas were selected. Six of these are in upland forest types. Two in Alabama are on sharply rolling terrain with steep slopes; yellow-poplar occurs on lower slopes and scarlet and southern red oak on middle slopes. Four upland areas in Mississippi are in the rich loessial bluffs bordering the eastern edge of the Mississippi Delta. Tree species sampled here included those in the Alabama areas and many in the bottom lands.

Of the 10 bottom-land areas, 1 is in a river bottom in Arkansas and 9 are within the floodplain of the Mississippi River; 8 of the latter are protected from river rises by the levee system. The terrain of the bottom lands is flat, and elevation differences of only a few feet markedly affect hardwood timber types. The soils vary from heavy clays on the poorly drained sites to silt loam and sandy loam on the better drained sites. Many tree species occur, but sweetgum and oaks dominate the commercial cut.

In these 16 areas data were taken on all dead branches (larger than 1 inch in diameter) found on tops left from recent commercial logging operations. In all, the main stems behind 1,696 dead branches were dissected. All data were gathered in 1957.

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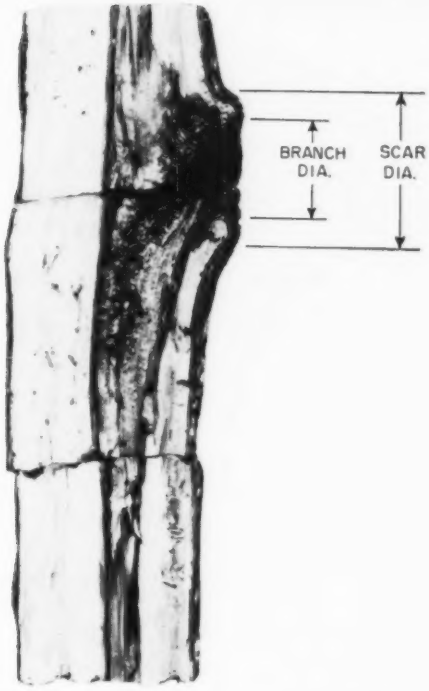

FIGURE 1. *Branch scar on sweetgum.*

In order to correlate the findings from top wounds with branch wounds lower in the stem, i.e., in the commercial logs removed, branch wounds and scars and the rot behind them were examined in 75 trees. These observations indicated that the proportion of large scars is less in the lower bole than in the upper bole, but that the other relationships described in this paper apply equally well to the lower bole.

Tree species sampled, ranges in the time the branches had been dead, branch diameters at death, and current wound or scar size, as well as length of rot in the main stem, are indicated in Table 1. The points used in measuring branch diameters are shown in Figure 1. The ages of the scars were determined by counting the age of callus tissue.

The 10 species or species groups that were represented adequately for analysis include most of the important southern hardwoods.

Blocks for culturing were taken from one location in each of the 196 rot columns sampled: other studies show that, as a rule, only one fungus occurs back of an individual wound. Identifications were checked by the U.S. Forest Disease Laboratory at Beltsville, Maryland; 90 of the 101 cultures were identified.

Results

Fungus species, years since branch death, and branch diameter affected the incidence and rate of decay. It was found that the extent of rot behind branches, wounds, or scars in a standing tree could be gauged by estimating the diameter of branch scar (Fig. 1) at time of observation and the number of years since the death of the branch.

Fungi causing decay. Soon after a branch dies its sapwood is infected by fungi. After decay fungi have penetrated the sapwood, heart-rot fungi become established (Fig. 2) and work into the trunk—or the fungus decaying the sapwood sometimes continues in the heartwood.

No more than one heart-rot fungus was isolated from behind any one branch or scar. Although 26 fungi were identified (Table 2), 4 species caused half of the identified cases of rot. *Stereum gausapatum*

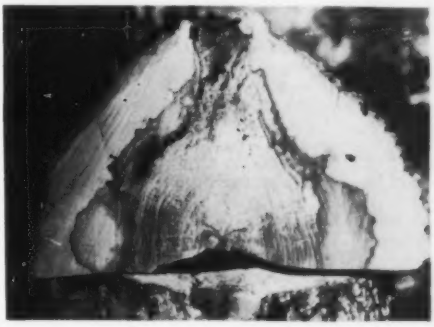

FIGURE 2. *Cross section through a branch scar on willow oak, showing the heart rot caused by* Poria andersonii.

was by far the most frequently isolated, followed by *Poria andersonii*, *Stereum subpileatum*, and *Pleurotus corticatus*. Roth (1948) found that *Stereum gausapatum* was the fungus most commonly infecting pruning wounds on oaks in Virginia. (One or more important rot fungi may have been missed in sampling trees for cultural identification.)

Fungi are known to vary greatly in the rates at which they spread within a tree. For 7 of those in the present sample (*Stereum gausaptum*, *Stereum subpileatum*, *Poria andersonii*, *Poria ambigua*, *Polyporus fissilis*, *Polyporus versicolor*, and *Pleurotus corticatus*), the annual rate of decay per inch of branch diameter (Table 2) for all tree species was compared by analysis of variance. The rate of decay of *Poria andersonii* was significantly greater, at the 5-percent level, than that of *Polyporus versicolor* and *Poria ambigua*. Other interspecies differences were not significant.

In the South the fruiting bodies necessary for field identification of many rot fungi are rarely seen on dead branches or

TABLE 1. Range in data on branch wounds and scars.

Species[1]	Branches		Time branch had been dead	Diameter of branch at death	Scar diameter	Length of rot in main stem[2]	
	Total	With rot in main stem				Above scar	Below scar
	Number		*Years*	*Inches*	*Inches*	*Inches*	*Inches*
Nuttall oak, *Quercus nuttallii* Palmer	402	83	2–28	1–6	2–9	0–126	0–138
Willow Oak, *Q. phellos* L.	286	75	2–39	1–11	2–14	0–108	0–93
Water Oak, *Q. nigra* L.	138	67	2–26	1–10	2–15	0–72	0–122
Cherrybark oak, *Q. falcata* var. *pagodaefolia* Ell.	137	52	1–28	1–10	3–10	0–236	0–86
White Oaks, *Q. lyrata* Walt., *Q. stellata* var. *mississippiensis* (Ashe) Little, *Q. alba* L., *Q. prinus* L., and *Q. michauxii* Nutt.	119	25	2–30	1–11	3–13	0–156	0–76
Yellow-poplar, *Liriodendron tulipifera* L.	105	21	2–28	1–4	2–7	0–21	0–109
Eastern cottonwood, *Populus deltoides* Bartr.	84	58	3–17	1–11	3–13	0–35	0–68
Upland red oaks, *Q. falcata* Michx. and *Q. coccinea* Muenchh.	82	22	2–58	1–6	3–8	0–41	0–65
Sweet gum, *Liquidambar styraciflua L.*	80	25	3–25	1–9	2–10	0–16	0–30
American sycamore, *Platanus occidentalis* L.	46	23	3–25	1–15	2–25	0–192	0–156
Water hickory and pecan, *Carya aquatica* Michx. L.) Nutt. and *C. illinoensis* (Wangenh.) K. Koch	52	8	3–28	1–6	2–8	0–5	0–34
American elm, *Ulmus americana* L.	39	15	4–25	1–4	2–7	0–35	0–46
Hickories, *Carya glabra* (Mill.) Sweet. and *C. ovata* (Mill.) K. Koch	27	7	3–15	1–5	2–7	0–39	0–57
Cedar elm, *Ulmus crassifolia* Nutt.	24	2	4–22	1–3	3–5	0–5	0–17
Green ash, *Fraxinus pennsylvanica* Marsh.	23	2	3–23	1–5	2–8	0–8	0–36
Sassafras, *Sassafras albidum* (Nutt.) Nees	18	5	4–21	1–3	2–6	0–66	0–50
American beech, *Fagus grandifolia* Ehrh.	11	1	4–10	1–3	3–6	0–36	0–10
Red maple, *Acer rubrum* L.	10	1	3–10	1–5	2–8	0–6	0–31
Honeylocust, *Gleditsia triacanthos* L.	5	4	7–12	2–3	4–6	0–11	0–21
Black willow, *Salix nigra* Marsh.	4	3	4–13	2–6	5–9	0–14	0–22
Boxelder, *Acer negundo* L.	3	3	6–9	3–4	5–5	7–22	14–48
Blackgum, *Nyssa sylvatica* Marsh.	1	1	12	2	4	10	26
Total or range	1,696	503	1–58	1–15	2–25	0–236	0–156

[1] Data for the first 10 species were subjected to detailed analysis.
[2] Measured from the point where branch wood entered the stem.

TABLE 2. Isolates identified from heart rot behind dead branches.

Fungi isolated	Cases	Annual spread of rot per inch of branch diameter
RED OAKS	*Number*	*Inches*[1]
Stereum gausapatum Fr.[2]	22	1.7 ± .2
Poria andersonii (Ell. & Ev.) Neuman[2]	8	2.8 ± .9
Stereum subpileatum B. & C.	6	1.6 ± .5
Polyporus fissilis B. & C.	4	2.4 ± .9
Polyporus versicolor (L.) Fr.[3]	4	.7 ± .2
Poria ambigua Bres.	3	.5
Pleurotus corticatus Fr.	2	1.3
Hydnum erinaceus (Bull.) Fr.	2	.4
Stereum complicatum (Fr.) Fr.[3]	2	1.3
Pleurotus ostreatus (Jacq.) Fr.[2]	2	.9
Peniophora sp.	2	1.1
Stereum frustulatum (Pers.) Fr.	2	1.1
Poria nigra (Berk.) Cooke	2	1.0
Polyporus adustus Willd. ex Fr.[3]	1	2.0
Polyporus delectans Peck.	1	6.6
Corticium lividum (Pers.) Fr.[2]	1	.5
Ptychogaster cubensis Pat.	1	1.5
Merulius tremellosus (Schrad.) Fr.[2]	1	.4
Polyporus compactus Overh.	1	2.0
Poria laevigata (Fr.) Karst.	1	1.2
Polyporus sulphureus (Bull.) Fr.	1	1.6
WHITE OAKS		
Stereum gausapatum Fr.[2]	4	.5 ± .1
Polyporus dryophilus Berk.	1	1.0
Pleurotus corticatus Fr.	1	4.8
Trametes rigida Berk. & Mont.	1	.4
COTTONWOOD		
Pleurotus corticatus Fr.	1	.3
Polyporus delectans Peck.	1	2.2
HONEYLOCUST		
Poria spiculosa Campbell & Davidson	2	1.0
Corticium lividum (Pers.) Fr.[2]	1	1.3
SWEETGUM		
Pleurotus corticatus Fr.	2	1.0
Lentinus tigrinus (Bull.) Fr.[2]	1	.8
RED MAPLE		
Ustulina vulgaris Tul.[2]	1	.7
YELLOW-POPLAR		
Polyporus versicolor (L.) Fr.[3]	1	.7
AMERICAN SYCAMORE		
Poria ambigua Bres.	1	.4
Lentinus tigrinus (Bull.) Fr.[2]	1	.3
Polyporus adustus Willd. ex Fr.[3]	1	.5
BLACK WILLOW		
Polyporus fissilis B. & C.	1	.8

[1] Mean ± standard errors are included for all classes with 4 or more cases.

[2] These fungi cause decay of both sapwood and heartwood.

[3] These fungi are primarily sapwood rotters, but attack heartwood to a limited extent.

scars. Identification, therefore, usually must be based on characteristics of the rot or of cultures obtained from it. *Stereum gausapatum* causes a white rot (Davidson 1934); in culture it can be identified by its microscopic characters. *Poria andersonii* rot (Fig. 2) is white, soft, and spongy (Campbell and Davidson 1939). *Stereum subpileatum* causes a honeycomb rot (Long 1915); in addition, freshly cut surfaces of both rotten wood and cultures have a distinctive sweet, musty odor. *Pleurotus corticatus* causes a white rot and, in culture, produces characteristic conidia borne on coremia (Kaufert 1935).

Hepting *et al.* (1940) found that the most common and important top-rot fungi in Appalachian oaks are *Stereum frustulosum* (*S. frustulatum*), *Polyporus dryophilus*, *Stereum gausapatum*, *Poria andersonii* and *Hydnum erinaceus*. All of these were isolated in this study but only *Stereum gausapatum* and *Poria andersonii* were among the commonly encountered species (Table 2).

Incidence of decay. Table 3 shows the relationship between the incidence of rot and branch diameter for 10 species or species groups. The proportion of branches infected was 11 percent for 2-inch branches, 36 percent for 3-inch branches, and 56 percent for 4-inch branches. The proportion of branch samples infected varied with species—the largest differences were in the small diameter classes. For example, in the 2-inch class, 54 percent were infected in cottonwood and only 1 percent in Nuttall oak.

Since branch wounds are gradually overgrown by callus tissue, the diameters of the original branches cannot be accurately estimated externally. However, the diameters of branch scars, either open or healed, are readily determined. The incidence of infection to be expected in the main stem behind branch scars on southern oaks is indicated in Table 4. Similar data for four diffuse-porous hardwoods are in Table 5. These species combinations were

TABLE 3. Proportion of branch samples associated with rot in the main stem, by species and diameter class.

Species	Diameter class											
	2 inches		3 inches		4 inches		5 inches		6 in. and over		All diameters	
	Total sample	Infected	Total sample	Infected	Total sample	Infected	Total sample	Infected	Total sample	Infected	Total sample	Infected
	No.	*Pct.*	*No.*	*Pct.*	*No.*	*Pct.*	*No.*	*Pct.*	*No.*	*Pct.*	*No.*	*Pct.*
Eastern cottonwood	48	54	24	83	8	100	2	100	2	100	84	69
American sycamore	12	25	21	62	6	33	–	–	7	71	46	50
Sweetgum	51	6	16	56	8	100	2	100	3	100	80	31
Upland red oaks	53	13	16	38	10	70	2	50	1	100	82	27
Yellow-poplar	90	16	11	45	4	50	–	–	–	–	105	20
White oaks	60	8	36	17	12	58	7	57	4	75	119	21
Cherrybark oak	36	11	63	29	22	77	10	60	6	83	137	37
Water oak	59	24	39	49	21	76	11	91	8	87	138	48
Willow oak	152	8	91	34	26	58	11	90	6	100	286	28
Nuttall oak	236	1	106	23	35	51	15	60	10	100	402	16
Total	797	11	423	36	152	56	60	73	47	89	1,479	29

TABLE 4. Rot infection behind branch scars on southern oaks (Nuttall oak, water oak, willow oak, cherrybark oak, upland red oaks, white oaks).

Scar diameter (inches)	Years since death of branch									
	Up to 5		6–10		11–15		Over 15		All	
	Total sample	Infected	Total sample	Infected	Total sample	Infected	Total sample	Infected	Total sample	Infected
	No.	*Pct.*	*No.*	*Pct.*	*No.*	*Pct.*	*No.*	*Pct.*	*No.*	*Pct.*
2	4	0	1	100	–	–	–	–	5	20
3	133	3	73	11	11	9	1	0	218	6
4	179	11	174	17	32	16	8	63	393	15
5	96	26	136	37	50	34	9	11	291	31
6	40	55	61	51	31	42	15	60	147	51
7	9	67	31	77	18	61	12	67	70	67
8	3	100	8	87	8	88	6	100	25	92
9	–	–	4	100	2	100	–	–	6	100
10[1]	1	100	–	–	2	100	6	100	9	100
All	465	17	488	32	154	37	57[2]	58	1,164	28

[1]Six samples 12–15 inches in diameter.
[2]All but 12 samples in 16-20 year class.

made to increase the usefulness of the tables, for species differences within the groups were not great enough to warrant separation.

On the oaks, likelihood of infection increases as years since death of the branch increase. With the diffuse-porous hardwoods there is a sharp increase to 10 years, but none in the older ages. Of the oak scars 8 inches or larger in diameter 92 to 100 percent were infected, but only 3 percent of the wounds sampled were this large. Likewise, 100 percent of the 7-inch or larger scars on the diffuse-porous hardwoods were infected, but such scars comprised only 8 percent of the total sample.

The sample of epicormic branches was too small to indicate whether incidence of infection was the same for them as for normal ones. There were no differences between open and healed scars. Incidence of infection varied somewhat between stands in the same location, and between trees of the same species in different locations, but the differences were not considered important.

TABLE 5. Rot infection behind scars on diffuse-porous hardwoods (yellow-poplar, sycamore, cottonwood, and sweetgum).

Scar diameter (inches)	Years since death of branch									
	Up to 5		6–10		11–15		Over 15		All	
	Total sample	Infected	Total sample	Infected	Total sample	Infected	Total sample	Infected	Total sample	Infected
	No.	*Pct.*	*No.*	*Pct.*	*No.*	*Pct.*	*No.*	*Pct.*	*No.*	*Pct.*
2	9	11	4	0	4	0	–	–	17	6
3	27	11	27	30	24	8	6	17	84	17
4	20	30	56	48	11	36	17	18	104	38
5	4	50	32	53	11	55	10	50	57	53
6	1	100	17	82	4	75	2	0	24	75
7	–	–	1	100	9	100	2	100	12	100
8	1	100	1	100	2	100	–	–	4	100
9	–	–	–	–	1	100	1	100	2	100
10+	1	100	1	100	2	100	2	100	6	100
All	63	24	139	50	68	43	40	35	310	41

Factors influencing rate of decay. The effect of geographic location on rate of decay was tested statistically for yellow-poplar in three locations and for Nuttall oak in six locations. No significant differences between locations were found for either spe-

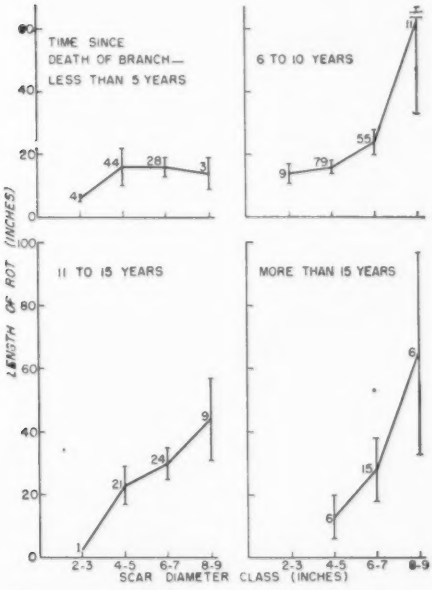

FIGURE 3. *Length of rot behind infected branch scars on southern oaks (Nuttall oak, water oak, willow oak, cherrybark oak, upland red oaks, and white oaks). Numbers beside points show how many scars the average is based on. Vertical lines indicate plus and minus standard errors of the means.*

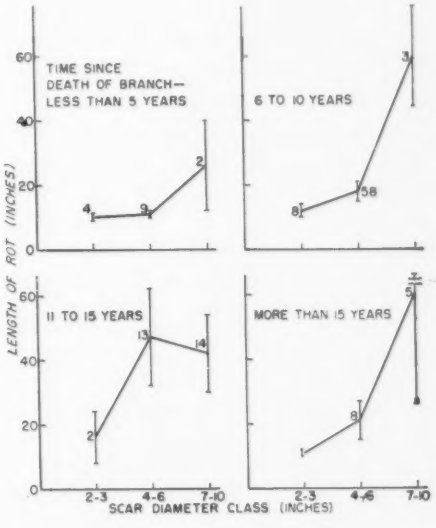

FIGURE 4. *Length of rot behind infected branch scars on diffuse-porous hardwoods (yellow-poplar, sycamore, cottonwood, and sweetgum). Numbers beside points show how many scars the average is based on. Vertical lines indicate plus and minus standard errors of the means.*

FIGURE 5. *Small branch scar (3 inches in diameter) on Nuttall oak. No rot was associated with this scar.*

cies, and, as there was little obvious variation for other tree species, no further statistical tests were made.

Branch diameter and years since death of the branch were correlated with the total length of the rot column in the main stem. Scar diameter was also correlated with rate of decay. To simplify field use of the information, the data on scar diameter and age for all of the oaks are combined in Figure 3, and those for 4 diffuse-porous species in Figure 4. For the oaks, length of rot behind infected branch scars increased with scar diameter, except when scars were less than 5 years old. For the diffuse-porous hardwoods there was an increase in length of rot with scar diameter for all but the 11- to 15-year age class.

Since epicormic branches often do not extend into the heart, it seemed possible that such branches would have less associated rot than would normal branches, but the number of branches of epicormic origin was too small to indicate if a relationship existed.

Most of the scars in this sample were open and did not have significantly more rot than healed scars. The healed scars averaged older than the open scars. The following tabulation shows the percentages of open and healed scars and their average ages:

	Healed scars		Open scars	
	(Percent)	(Age in yrs.)	(Percent)	(Age in yrs.)
Oaks	24	12	76	6
Diffuse-porous species	36	12	64	5

Length of dead stub (when a stub was present) was not related to length of rot.

Discussion

Abundant observations indicate that most of the rot that leads to cull in commercial southern hardwood logs enters through basal wounds, principally those resulting from fire. It has been estimated that less than 20 percent of the loss from decay in southern hardwoods is associated with

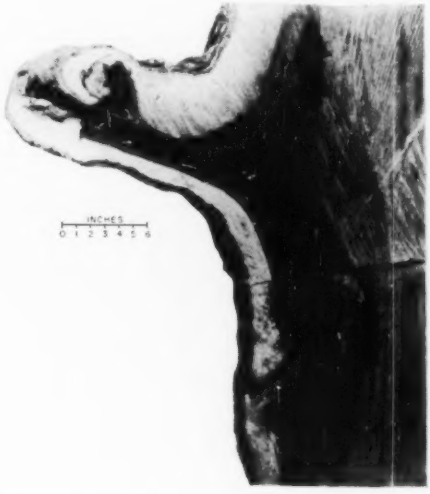

FIGURE 6. *Large old branch scar on white oak, split open to show rot.*

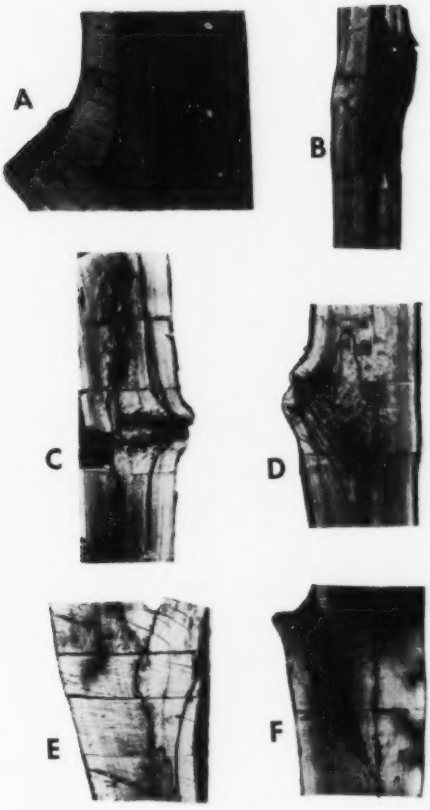

FIGURE 7. *Vertical sections through large branch scars. Limits of visible rot are outlined in black. A, C. Recent scars on willow oak. Fungus in C is* Poria andersonii. *B. Recent scar on sweetgum, infected by* Pleurotus corticatus. *D. Old scar on southern red oak, infected by* Corticium lividum. *E, F. Recent scars on water oak. Rot is limited to the branch wood.*

branch wounds (Hepting *et al.* 1940, and general observations). The present study shows that the primary reason for the low amount of cull associated with branch scars is that most such scars are small (Fig. 5) —and little decay occurs behind a small scar unless the branch has been dead for many years. Eighty-three percent of the scars in this sample were 3 inches or less in diameter. Only 3 percent of the scars were in the high-hazard class, i.e., 6 inches or more in diameter (Fig 6). Nevertheless, the study shows that, in individual trees or stands with a high proportion of large branch wounds, the associated rot can be important. This would be particularly true with a greater use of top wood.

The field observer or timber cruiser can readily estimate diameter of a branch scar to the nearest 2 or 4 inches, but will find it difficult or impossible to estimate, even to the nearest 5 years, the time that the branch has been dead. In Table 6 the data from Tables 4 and 5 and Figures 3 and 4 are arranged in 3 scar-size classes and 2 age classes. To use the table the observer need only judge whether the scar is small (present diameter 1 to 3 inches), medium (present diameter 4 to 6 inches), or large (present diameter 7 to 10 inches), and whether it is recent (less than 15 years old) or old (between 15 and 30 years). With this classification of age and size, the observer may read from the table the average linear extent of rot to be expected behind scars.

It is helpful to keep in mind that scars with dead stubs still attached are always less than 15 years old and are unimportant unless they are large. There is no important

TABLE 6. Average length of rot to be expected in the main stem behind branch scars of various sizes and ages.

Tree-species and age of scar[1]	Small branch scars[2]	Medium branch scars[2]	Large branch scars[2]
	Feet	*Feet*	*Feet*
Oaks			
Recent	0.1	0.4	2.5
Old	.2	1.0	5.7
Diffuse-porous hardwoods			
Recent	.2	.9	3.6
Old	.2	.9	5.0

[1] Recent branch scars are less than 15 years of age, old scars between 15 and 30 years.

[2] Present diameter of:
Small branch scars = 1 to 3 inches
Medium branch scars = 4 to 6 inches
Large branch scars = 7 to 10 inches

amount of rot in the heartwood behind scars 1 or 2 years old. Healed scars will be 5 or more years old.

The length of rot up or down from any scar would be one-half the amount indicated by Table 6, for rot advances with equal rapidity in either direction.

Once the rot fungus enters the branch stub, it spreads into the main stem through the branch wood (Fig. 7, E and F). In the stem, horizontal spread is much slower than vertical spread (Fig. 7, A, B, C, and D; and Fig. 2). Therefore, until rot is well established only a small part of the stem cross section is cull.

As a further aid in the application of these data, the following rules of thumb are accurate enough for practical use in estimating cull from top rot:

1. Disregard small and medium scars. Even if they are infected, volume deduction will be less than 10 board feet.
2. For large, recent scars, deduct one-half of the board-foot volume of the part of the log with rot.
3. For large, old scars, deduct all of the board-foot volume of the part of the log with rot.

Although branch scars may not often have important cull associated with them, they must always be considered as a defect because knots are associated with them.

Summary

The stems behind 1,696 dead branches on important southern hardwood tree species from 16 study areas in Alabama, Mississippi, and Arkansas were dissected and analyzed for heart rot. Rot was associated with 29 percent of the samples.

Although 25 fungi were identified, 4 species caused 52 percent of the identified cases of rot. These were *Stereum gausapatum* (29 percent), *Poria andersonii* (9 percent), *Stereum subpileatum* (7 percent), and *Pleurotus corticatus* (7 percent). Rate of decay varied with fungus species, branch diameter at time of death, branch scar diameter at time of sampling, and years since death. These relationships varied somewhat among tree species or groups of species.

Over 80 percent of the branches sampled were 3 inches or less in diameter. Few branches of this size had much rot behind them, but a high percentage had infections that eventually would cause significant amounts of rot.

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Air-Layering of Lodgepole Pine and Origin of Adventitious Roots

BY
KYONG BIN YIM

ALTHOUGH any one of the three important vegetative propagation methods, cuttings, grafting, and layering, transmits the identical genetic characters of the ortet, each method has advantages and disadvantages. The multiplication of desired materials by cuttings or grafting is often preferable to layering if the cuttings root easily or if a satisfactory proportion of the grafts succeed.

Layering, however, does not need the close attention to environmental factors required by cuttings. Increased rooting can be expected to result from an abundant supply of water to the air-layered branches through the girdled tissue, and of photosynthate beyond the girdle. There is also less shock than with cuttings.

Relatively good lodgepole pine (*Pinus contorta* var. *latifolia* Engelm.) stands are growing on the Suwon Agricultural College Forest, Suwon, Korea. In the course of vegetative propagation studies on several coniferous species by the author, an attempt has been made during 1959 to test the feasibility of air-layering lodgepole pine.

Review of Literature

An old Korean text (Chung 1826) describes layering techniques, as well as cutting and grafting in considerable detail. The air-layering method is described as follows: After fine yellow soil of good quality is dried and screened, some urine is added. This sequence, drying, screening, and adding urine, is repeated more than ten times to prepare the root-stimulating substance. The practice then is to place a layering pot made of bamboo stem full of the mixture of fine clay and the specially prepared yellow soil as the rooting media about the branch at the desired rooting point, making frequent irrigations.

In view of the findings that the crystalline auxin preparations prepared by Kögl and co-workers from urine show root forming activity, and that when auxin destruction is partial, the root-forming activity is comparably reduced (Thimann 1935), the above-mentioned method seems reasonable.

Rooting ability of the ramets from aged ortets often give poor results whereas good success may be attained with younger ones (Cech 1955, Hoekstra 1957). Singh (1953), however, stated that mango (*Mangifera indica* L.) shoots can be air-layered successfully from quite old mother trees, provided the shoots are in active physiological condition and the right concentration of plant hormones is applied to them.

A comprehensive literature review on the vegetative propagation of forest trees has been made recently (Nienstaedt *et al.* 1958).

Materials and Methods

Sixteen 8-year-old lodgepole pines growing vigorously in rows were selected and divided into four blocks of four trees each. The number of air-layered branches in each block was 40 since ten air-layers were put on each tree in this experiment. Branches

The author is Assistant Professor in Suwon Agricultural College, Korea. He wishes to express his appreciation to Shin Kyu Hyun for assistance in various phases of the study, and to Donald P. Duncan for reviewing the manuscript. Manuscript received July 18, 1960.

for treatment were chosen only from the second and third whorl branches counting from the top. The girdle was made on the terminal shoot. The four possible combinations of two plant hormones and two application dates were applied within each block. All 40 branches were assigned the four treatments at random so that ten air-layers in a block were subjected to the same treatment combination.

The first 80 air-layers were made on June 17, the remaining 80 air-layers on July 8. Thus a total of 160 air-layers were made on 16 lodgepole pines. In all of the 80 air-layers made on the same date, 40 were treated with 1.2 percent (by weight) indole butyric acid and the other 40 with 1.2 percent indole acetic acid.

The girdles were 0.5 cm wide and were located some 10 cm from the tip of the branches. Stripping of the needle fascicles was usually necessary, but was held to a minimum. Great care was taken not to harm the xylem but to affect complete removal of the bark. The girdled xylem including the upper rim all around the branch was dusted with one of the two 1.2 percent plant hormone-talc mixtures. A handful of moist moss was wrapped around the treated part and covered with a polyvinyl plastic sheet measuring 20 x 20 cm.

Results and Discussion

Two months after treatment, all air-layered branches were cut and the wrapping materials were removed to inspect rooting. Damaged air-layers, including the dried ones with roots, were omitted from the calculations. Roots with more than normal development of lignified epidermis, showed adaption to drought resistance and were deep brown in color. Whatever air-layers survived until the counts were made produced at least some roots.

The results are presented in Table 1 where the numbers of rooted branches have been grouped by date and plant hormone.

The observed data expressed in percent rooting were transformed by angular transformation (Snedecor 1956) and subjected to analysis of variance. Differences between hormones were nonsignificant (probability greater than 5 percent), as was interaction between hormones and application dates. However, significant differences between dates of application resulted.

TABLE 1. Effect of plant hormone and application date on rooting of lodgepole pine air-layers (in percent of rooted branches).

Date	Treatment	
	IAA	IBA
June 17	85.0	65.0
July 8	27.5	40.0

Average rooting percentage was 54.4 and the highest was 85.0 for the 1.2 percent indole acetic acid treatment on June 19. Nearly all roots grew in the direction of the branch tip, probably as a result of a geotropic response to the droop of the air-layered branch. The stem distal from the girdle showed a noticeably expended growth in diameter, but the stem below the girdle, with its lack of cambium, retained the original diameter and became brittle. The reason for the noticeable radial growth of the stems might be accounted for by the activated cambial function from the exogenous application of plant hormones. It is known that native auxins move almost entirely in a basipetal direction but synthetic auxinlike substances can move up through the xylem into the leaves, and from there they may be re-routed via the phloem (Hitchcock and Zimmerman 1935, Zimmerman and Wilcoxin 1935, Oserkowsky 1942).

Therefore, their translocation pattern is both polar and apolar; transport into the air-layered portion toward the branch tip from the girdled part takes place through the xylem, even through dead tissue. The present author's observation is in agreement with Reines' findings (1959) that the retardation and stimulation of cambial ac-

tivity resulted from the different amount of plant hormone in portions above and below the girdle in black cherry (*Prunus serotina* Ehrh.).

As soon as the assessment of rooting was finished, the branches were planted in a propagating frame covered with lath-screens. The frame was filled with fine river sand. The amount of irrigation was increased as time went on, so as not to give them too sudden a change in moisture condition.

Very rapid root elongation continued in the frame and the needles took on a healthier green color. It is thought that removal of rooted air-layers from the tree at two months after treatment, is too late. In many cases, conspicuous curled development of the roots in the ball of moss, indicated lack of sufficient room to grow.

This experiment reveals that lodgepole pine air-layering is feasible and that good results can be expected. Moreover, with similarly successful results in pitch pine (*Pinus rigida* Mill.) air-layering obtained in 1959 by the author (unpublished), there is evidence that air-layering in many pine species may be practical.

Origin of Roots

Satoo (1952, 1955, 1956) found adventitious root-origins in the seedling cuttings of five pine species (*Pinus densiflora*, *Pinus Thunbergii*, *Pinus silvestris*, *Pinus pinaster* and *Pinus strobus*), in the callus tissues of the decayed portion near the cut base over the cut surface except for the white pine (*Pinus strobus* L.) which had origins in the bud traces. Bannan (1941, 1942) observed root origin in the layered material of several coniferous species collected from the field. Mergen (1955) found in an air-layering study of slash pine that all adventitious root origins were from the base of the "wound or repair wood" which had been laid down along the lower part of the branch toward the tip from the girdle.

As an approach to finding reasonable air-layering procedures, investigation of root origin in lodgepole pine was made with the ten samples collected on the September 8. A branch about 2 cm long around which roots were produced, was severed and soaked in FAA killing solution (Sass 1951) for a week, and 30-micron sections were stained with safranin and Delafield's hematoxylin. With this stain, the identification of so-called "wound wood" or "newly formed xylem" became clear. The following three cases in adventitious root origin were confirmed.

Case 1. As has been discussed before, the cross section of the expanded basal part of the upper section of the girdle showed much irregularity in tissue development, because of the girdling and plant hormone treatment. This agrees with Delisle's (1939) finding of histological disorder in rooting cuttings of the white pine (*Pinus strobus*) induced by indoleacetic acid, viz., cambial activity was not uniform throughout. As shown in Figure 1, the root primordium appears to develop simultaneously along with secondary xylem directly from the cambium and has very little direct connection with the last year tissues. In a large mass of parenchymatous cells, those cells with visible development of a cell membrane, lined up radially, are the constituents of the root primordium. As further differentiation proceeds, the primordium pushes on the cortex and finally a protruding root appears.

Case 2. This is similar to the case observed by Mergen (1955) in rooted slash pine air-layers. Figure 2, though it shows the very late stage of adventitious root formation, portrays continuous vascular connections between the xylem of the roots and the xylem or secondary tissue of the branch which has been produced by the wood cambium after the girdling. Distinction between the xylem of the branch before girdling and the wound xylem was easily drawn because of differing degrees of staining. This kind of root formation was mostly observed at the basal portion of wound xylem. Root xylem was surrounded by

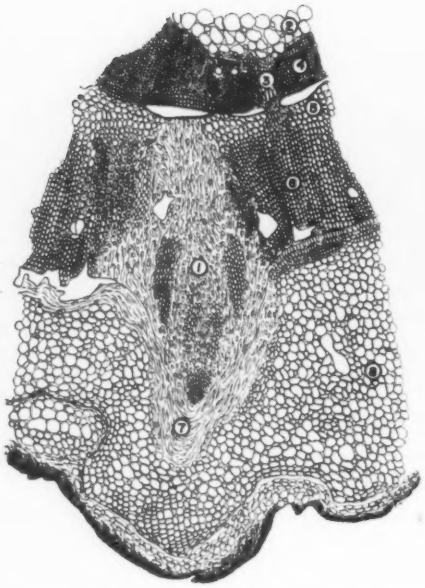

FIGURE 1. *Camera lucida drawing of root-primordium developed from xylem tissue formed in the second year. 1. Root primordium. 2. Pith. 3. Leaf trace. 4. Secondary xylem formed in the first year (1958). 5. Spring wood in the second year (1959). 6. Summer wood in the second year. 7. Compressed parenchymatous tissue. 8. Cortex.*

thick parenchymatous callus tissue with cork-cambium outside.

Case 3. This is different from case 2, where the root-primordium originated from callus tissue formed below the wound xylem. In case 3, a pocket of parenchyma cells in the xylem tissue formed before the girdling, was differentiated into a root-system (Fig. 3). The development of the meandering wound xylem was produced chiefly during the time the cuttings were in sand medium, after being severed from the ortet. Finally, the wound xylem is penetrated by the emerging root-primordium.

Without exception, in the course of development of primordia, some tissues disappeared or were merged into others. Isolated and unorganized vascular elements, which were scattered throughout the meristematic mass made connection with the

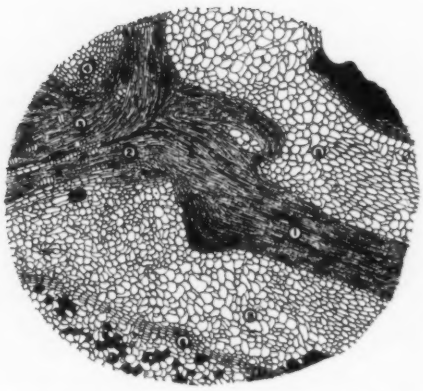

FIGURE 2. *Camera lucida drawing of radial section of rooted air-layers. 1. Xylem of adventitious root. 2. Wound xylem. 3. Xylem of branch before girdling. 4. Pocket of parenchyma cells produced in xylem of branch. 5. Parenchymatous callus tissue. 6. Cork cambium.*

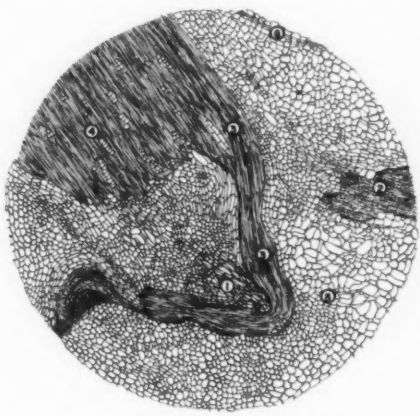

FIGURE 3. *Root-primordium developed in connection with parenchymatous tissue surrounded by secondary xylem formed before girdle. 1. Root primordium. 2. Callus xylem. 3. Wound xylem. 4. Xylem of branch before girdling. 5. Parenchymatous callus tissue. 6. Cork cambium.*

vascular system of the branch, in due course.

In conclusion, in lodgepole pine air-layers, adventitious roots arose from the secondary xylem tissues formed before or after girdling, and also from the callus tissues. In this investigation, no consideration was given as to preferred portion of the stem for making the girdle.

Summary

A total of 160 air-layers on 16 8-year-old lodgepole pines were made at Suwon, 80 on June 17 and 80 on July 8, 1959. The plant hormones used were 1.2 percent (by weight) indole butyric acid and 1.2 percent indole acetic acid in a talcum powder carrier.

The data were obtained two months after treatment. Significant differences between dates of application but nonsignificant differences between the two plant hormones resulted. The maximum rooting percentage was 85, following treatment with 1.2 percent indole acetic acid on June 17.

Histological investigation showed that adventitious roots developed from the cambium along with the secondary xylem of the current year's growth, and from parenchymatous callus tissues.

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Reduction in Peak Discharges Associated with Reforestation

BY
WILLIAM J. SCHNEIDER

DURING the early 1930's, the New York State Conservation Department purchased more than 340,000 acres of abandoned farmland within the State for the planting, growing, and harvesting of trees in perpetuity. This submarginal farmland, reforested mostly with conifers, is now dense woodlands with trees averaging about 30 feet high.

In 1932, the U. S. Geological Survey, in cooperation with the New York State Conservation Department, initiated a comprehensive program to study the effect on streamflow of reforesting the abandoned farmland. This paper describes the investigation of the effect upon peak discharges of the partial reforestation of the Shackham Brook area in central New York. A final report (Schneider and Ayer 1961) on the effect on all phases of streamflow also has been completed and is in press.

Description of the Study Areas

An experimental area was established in 1932 in the Shackham Brook watershed. Shackham Brook at its gaging point near Truxton, New York, drains 3.12 square miles. The area lies about 30 miles northeast of Ithaca in the glaciated Southwestern Plateau, at elevations ranging from about 1,290 feet to slightly over 2,000 feet above sea level. Shallow Pleistocene deposits of glacial till ranging from about 2 feet deep along the ridges to about 20 feet deep in the valley cover a bedrock of unaltered shales and limestones of Devonian age. Soils consist mainly of Lordstown and Volusia silt loams which are derived from the glacial till. The Lordstown soils have moderately good drainage, but the Volusia soils have a compact fragipan at shallow depth which usually results in excessively wet soils in the spring, along with perched water tables and hillside seeps.

Annual precipitation in the Shackham Brook area averaged 41 inches for the period 1934-57 and was distributed fairly uniformly by months. Snowfall averages over 80 inches per season and occurs from November through April.

An area drained by Fall Creek near Ithaca, New York, originally was designated as a control for the Shackham Brook area, but was abandoned after several years because of the poor correlation of the two streamflow records. In 1938, a new control area was established in the Albright Creek basin, about 8 miles southwest of the Shackham Brook area. Albright Creek at the gaging station at East Homer, New York, drains 7.08 square miles. The basin is similar to the Shackham Brook basin in topography, soils, geology, and other basin characteristics. About 20 percent of the area is in second-growth, mixed-deciduous woodland; the remainder is pasture and crop land. There has been no significant change in land use in the Albright Creek area during the study period. Streamflow from the Albright Creek area is compatible with that of other nearby areas which have not experienced drastic changes in land use.

Reforestation of Shackham Brook Area

Between February 1931 and April 1933, 1,146 acres, or 58 percent of the total area

The author is Hydraulic Engineer, U.S. Geological Survey; publication authorized by the Director of that agency. Manuscript received Oct. 4, 1960.

of the Shackham Brook watershed, were reforested. Because the land had been acquired by parcels, the reforested portions of the watershed did not follow natural boundaries, but instead followed the land-lines of farm tracts acquired by the State of New York. The reforestation, therefore, follows an irregular pattern (Fig. 1). This reforestation reduced the amount of pasture and cropland in the basin from 74 to 16 percent. Correspondingly, the coniferous woodland increased from one to 57 percent, and the deciduous woodland from 25 to 27 percent.

The reforested areas were hand planted with three- to four-year-old transplants. Little, if any, of the original ground cover was disturbed in planting. Records of the New York State Conservation Department indicate that about 1,250,000 trees were planted in the Shackham Brook watershed in about the following proportions according to species: 40 percent Norway spruce (*Picea abies*), 21 percent white pine (*Pinus strobus*), 16 percent Scotch pine (*Pinus sylvestris*), 11 percent red pine (*Pinus resinosa*), 6 percent European larch (*Larix decidua*), 4 percent balsam fir (*Abies balsamea*), and 2 percent black cherry (*Prunus serotina*) and black locust (*Robinia pseudoacacia*). Subsequent replantings of about 400,000 trees, mostly red pine, white pine, and Norway spruce, were made in 1934, 1936, and 1939.

The trees were permitted to grow without cutting or thinning, and there were no losses from forest fires. A field survey in 1958 indicated that the various plantings ranged from 4 to 7 inches d.b.h. and from 18 to 30 feet in height. The survey also indicated that almost complete crown closure had been obtained.

Approach to the Analyses

Collection of data in the Shackham Brook area began at about the same time as the reforestation. An adequate control area was not established until five years later. During this period, however, many of the

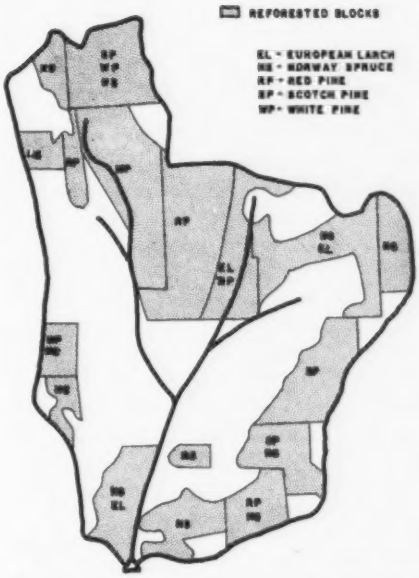

FIGURE 1. *Reforestation in the Shackham Brook area.*

original plantings in the Shackham Brook area had died, and subsequent replantings of almost one-third of the original total were made at about the time data collection was begun in the Albright Creek control area.

Thus the effect of the reforestation of Shackham Brook area can be measured from 1938, realizing of course that some small effect probably occurred during the 1932-37 period. However, any effect attributed to the reforestation subsequent to 1938 will therefore be a conservative estimate of the total effect. By not accounting for the 1932-37 period, the analyses as made may tend to underestimate the effect of the reforestation.

There is no pre-reforestation calibration period for the Shackham Brook and Albright Creek areas: changes in the Shackham Brook area attributable to the reforestation were assumed to have occurred gradually as a result of the tree growth and therefore would increase in the manner of a time trend.

In the subsequent analyses of peak discharges, the effect of reforestation is assumed from 1938, and changes in streamflow are measured from that date.

Analyses of Peak Discharges

The peak discharges of Shackham Brook were related to the peak discharges of Albright Creek to determine changes in the relationship between the two areas by using time as a third variable in a multiple-regression analysis. Both annual peaks and concurrent peaks were studied. The maximum discharge, termed the annual peak, was tabulated for each water year ending September 30. For the concurrent peak study, all peak discharges above a base of 10 cfs per square mile on Albright Creek were tabulated for the period November 1 to April 30. Each concurrent peak discharge on Shackham Brook was then tabulated regardless of its magnitude. The concurcurrent peak discharge was identified as that peak occurring from the same meteorological events as the peak on Albright Creek.

A similar tabulation was made for the period May 1 to October 31 for peaks above 2 cfs per square mile on Albright Creek. A total of 118 peaks for the November 1 to April 30 period and 25 peaks for the May 1 to October 31 period were tabulated. Analysis of all peak discharges on both areas indicated that only two peaks in the former and one peak in the latter period exceeded the comparable base on Shackham Brook but not on Albright Creek. These were not included in the tabulation.

The selection of the two periods for study was based on several factors. First, the periods November 1 to April 30 and May 1 to October 31 coincided approximately with the dormant and growing seasons in central New York. Although the growing season usually ends with killing frosts in September, hydrologic conditions exist into October which more resemble those of the growing season. The two periods also are characterized by a difference in types of precipitation. Precipitation during the period November 1 to April 30 results mainly from frontal activity, and is fairly uniform over the basins. Much of the precipitation, however, during the period May 1 to October 31 occurs as thunderstorms and is extremely variable over the basins. The period November 1 to April 30 also defines that period when snowfall and snowmelt are factors affecting the peak discharges. These periods also coincide with those used by Johnson and Kovner (1956).

Multiple-regression time-trend analyses were made using the model equation

$$\log S = a + b_1 \log A + b_2 T$$

where S is the peak discharge in cubic feet per second on Shackham Brook, A is the associated peak discharge on Albright Creek, and T is the position of the peak in a numerical sequence. For the study of the annual peaks, the numerical sequence followed the chronological sequence of years with the value one assigned to the 1939 water year. The numerical sequence also followed the chronological sequence for the concurrent peak study, the value one being assigned to the 6-month period ending April 30, 1939 for the dormant season peaks and to the 6-month period ending October 31, 1959 for the growing season peaks. The model was selected on the basis of a comparison of standard errors using several different types of model equations.

The analysis of annual peaks gave a regression equation of

$$\log S = + 0.853 + 0.633 \log A - 0.019 T \qquad (1)$$

The coefficient of T was tested as described by Ezekiel (1940) and determined significant well above the 99 percent confidence level. The relationship is shown graphically in Figure 2. The regression indicates an average reduction of 55 percent in annual peaks of Shackham Brook between 1939 and 1957.

Analysis of 118 pairs of concurrent peak discharges for the dormant, or winter, season of November 1 to April 30 gave a regression equation of

$$\log S = -0.133 + 0.977 \log A - 0.012\ T \qquad (2)$$

This relationship is shown in Figure 3. The coefficient of T was determined significant above the 99 percent confidence level, indicating a systematic reduction in the peak discharges of Shackham Brook between 1939 and 1957 for the dormant season. This reduction amounts to 41 percent for the 19-year period. For the growing season of May 1 to October 31, the correlation of 25 pairs of concurrent peak discharges gave a regression equation of

$$\log S = -0.877 + 1.358 \log A - 0.010\ T \qquad (3)$$

in which the coefficient of T was determined significant at the 85 percent confidence level. The trend as shown in equation (3) indicates a reduction of 33 percent in peak discharges of Shackham Brook for the growing season. The data for the growing season scattered widely because of large differences in thunderstorm rainfall within the basins during this season. Because of these intra-basin differences, consideration of rainfall data did not improve the relation between peak discharges for the growing season.

The relationship for the period November 1 to April 30 was further studied to detect any changing trend within the period. This was accomplished by analyzing the data separately for each month during the period. Graphical correlations indicated reductions ranging from about 70 percent in November to about 20 percent in April.

All peaks were therefore considered in one analysis, and the changing trend within the six-month period was expressed in the model equation . . .

$$\log S = a + b_2 \log A + b_3\ T + b_4\ D + b_5\ TD$$

in which the symbols S, A, and T are as previously described, and D is the number of days after November 1 to the date of the peak. The regression based on all concurrent peak discharges was computed as

$$\log S = +0.012 + 0.986 \log A - 0.028\ T - 0.00151\ D + 0.000143\ TD \qquad (4)$$

in which all terms were determined significant above the 99 percent confidence level. The effect of the date of occurrence on the relationship between the peak discharges of Shackham Brook and Albright Creek as described by the above equation is shown

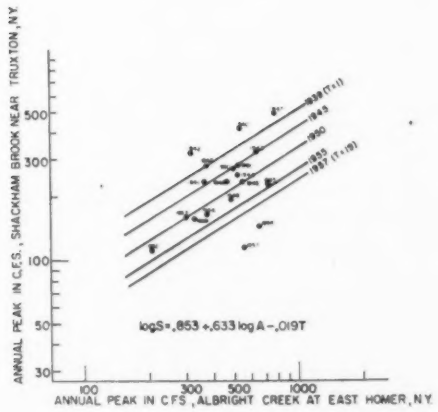

FIGURE 2. *Relation between annual peak flows of Shackham Brook and Albright Creek, 1939-57.*

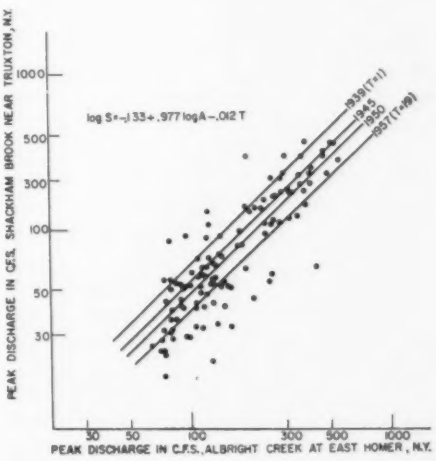

FIGURE 3. *Relation between peak flows of Shackham Brook and Albright Creek for the 6-month period ending April 30.*

in Table 1. The data in the table are average figures for the month, and indicate that reduction in peak discharges of Shackham Brook is greatest in the early part of the 6-month period, and decreases to a minimum in the latter part. The indicated reduction for November through April is 44 percent which agrees well with the 41 percent indicated by equation (2).

Further study of the data indicated a lesser degree of correlation in the later years in the relationship between the concurrent peak discharges of Albright Creek and Shackham Brook occurring during the spring months. Therefore, the relationship between peak discharges occurring in March and April of 1939-44 was compared with the relationship between peak discharges of March and April of 1952-57. This relationship was expressed as a ratio of the peak discharges. Because equation (2) indicated that the exponent of the relationship between peaks on Shackham Brook and Albright Creek was essentially unity, a direct ratio of the peak on Shackham Brook to the concurrent peak on Albright Creek was used. There were 18 samples in the early period and 19 in the latter. Each of the two groups was considered homogeneous, although it was recognized that there was some trend within each 5-year period. It was also recognized that some change due to reforestation had occurred by 1944. However, use of the period 1939-44 as indicative of pre-reforestation conditions should result in a conservative estimate of change.

Graphical plotting indicated that the data in each group approximated a log-normal distribution. The mean and standard deviation for each set of data based on the log-normal distribution were computed (Table 2). The data in this table indicate that although a general reduction is indicated in peak discharges of Shackham Brook from March and April of 1952-57, there is a significantly greater variance in the distribution of the ratios for the latter period.

The distributions of the ratios for the two periods were therefore studied by comparing their cumulative frequencies. A log-normal plotting of the cumulative frequency distributions indicated that at one common point in the cumulative distributions, the values of the ratios for both distributions were equal. At frequencies below that point, the values of the ratios in the distribution for the latter period were below those for the early period; above that point, they were higher. The common point at which values of the ratio were equal was expressed in terms of the parameters of the two distributions as

$$X_1 + k\sigma_1 = X_2 + k\sigma_2 \qquad (5)$$

where X is the mean of the distribution and σ is the standard deviation. Using the sample estimates given in Table 2, we find that at $k = 1.05$, the values of the ratios are equal in both distributions. From statistical tables of values of the normal distribution, we find that $X + 1.05\sigma$ corresponds to the 85 percent point in the cumulative frequency distribution. Thus, as indicated above, 85 percent of the ratios, or about six out of seven, are relatively lower the latter period, while 15 percent, or about one out of seven, are relatively higher.

TABLE 1. Reductions in peak discharges of Shackham Brook near Truxton, N. Y. between 1939 and 1957.

Month	Average reduction in percent
November	65.5
December	59.0
January	50.7
February	40.6
March	29.9
April	15.6

TABLE 2. Statistical parameters of peak discharge ratios.

Statistic	1939-44	1952-57
Mean ($\bar{x}$), in log units	.509	.395
Std. deviation, in log units	.116	.224

This indicates that, although in general peak discharges have been reduced, an occasional peak—about one out of seven—is now relatively higher than prior to the reforestation.

Data for the latter period also were studied to determine whether a relationship existed between the ratio as described above and the actual magnitude of the peak discharge. No significant relationship was found, indicating that the peaks on Shackham Brook occurring in the latter period, which are now relatively higher than those on Albright Creek, can be associated with peak discharges of any magnitude, large or small.

Summary of Results

Average reductions in peak discharge for winter and spring, ranging from 66 percent in November to 16 percent in April, have resulted over a period of 19 years from the partial reforestation of the Shackham Brook watershed. Annual peak discharges were reduced by an average of 55 percent. Reduction of 33 percent for summer and fall also were indicated by the analyses.

Although reductions are indicated for six out of seven peak discharges occurring during March and April, an average of one peak out of seven is now relatively higher on Shackham Brook during these months than during the early period following reforestation, but this peak may be of any magnitude.

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Stand Development and Soil Fertility in a Douglas-Fir—Red Alder Plantation

BY
ROBERT F. TARRANT

RED ALDER (*Alnus rubra* Bong.) is one of the most widely distributed hardwoods in the Douglas-fir region of the Pacific Northwest. On moist bottom-land sites, it normally occurs in pure stands and attains merchantable size. It is also abundant throughout the region as a noncommercial-sized tree on upland sites at elevations below about 3,000 feet.

Early growth is very rapid, and on good sites first-year seedlings may be as tall as 18 inches. Five-year-old alders may be 15 feet tall, and at 10 years their height may reach 35 to 40 feet (Worthington 1957).

Red alder is usually the first tree to become established following clear cutting if a seed source is present. Because of its rapid early growth, it often dominates associated conifer seedlings during early years of stand development. Thus, when alder reproduces naturally on upland sites on which it is unlikely to attain commercial size, it may seriously impede establishment of other tree species. In such circumstances, alder is regarded as a serious hindrance to full forest production.

On the other hand, alder is often considered a soil-improving tree species, and for this reason is believed by many to be a valuable stand constituent.

The widespread occurrence of alder in the Douglas-fir region and the divergence of opinion on the tree's silvicultural value emphasizes the desirability of learning more about the role of alder in soil development and its effect on Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) when the two species are grown in mixture.

Previous Investigations

Because alder often hinders conifer establishment on upland sites, considerable attention has been given to methods of control (Hawkes 1953, Ruth and Berntsen 1956). In addition, a number of studies have been made of the part it plays in improving forest soils.

It has long been known (Kellerman 1910) that *Alnus*, together with a few other non-legume genera, regularly bears root nodules that, by their perennial habit and repeated branching, eventually develop into clusters of considerable size. Though identity of the endophyte of *Alnus* nodules remains uncertain, evidence has accumulated—particularly from European studies—that the nodules resemble those of legumes in that they are nitrogen-fixing (Bond *et al.* 1954).

Johnson (1917) reported empirical observations of the soil-improving nature of red alder litter. More recently, red alder foliage has been shown to contain much greater amounts of nitrogen than that of other Pacific Northwest tree species (Tarrant *et al.* 1951).

Stone (1955) cites the European practice of including alder as a nitrogen-fixing tree species when planting difficult sites. He mentions that growth response of poplar was similar whether alder was included in the plantation or inorganic nitrogen

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fertilizers were applied.

Crocker and Major (1955), studying a recently deglaciated area in Alaska, found the mean annual net accumulation rate for nitrogen to be 55 pounds per acre during the period of plant succession in which *Alnus crispa* (*A. sinuata* (Reg.) Rydb.) was dominant. The rapid build-up of soil nitrogen throughout the alder thicket stage and the sharp reduction in soil nitrogen beneath young spruce following elimination of alder were cited as "very strong evidence for the fact that the mycorrhizal nodules on the roots of alder do have the capacity for nitrogen fixation."

Lawrence (1958) observed that on infertile, raw soil material exposed after the retreat of glaciers in Alaska, pioneer willow and cottonwood trees lie prostrate and have sickly yellow leaves. With the entrance of Sitka alder (*A. sinuata* (Reg.) Rydb.) into the succession, shrubs and trees previously of low vigor are stimulated to strong, erect growth. This increase in vigor is attributed to addition of nitrogen to the soil through nodular fixation on the alder root system. Stands of alder 5 years of age, averaging 5 feet in height, were found to add 140 pounds of nitrogen per acre to the soil annually.

Virtanen (1957) reported a study in which seedlings of *Picea abies* (L.) Karst. were grown for 11 years in quartz sand in association with nodulated *Alnus glutinosa* (L.) Gaertn seedlings. He found that even during the first years of growth, the seedlings obtained nitrogen fixed in the alder root nodules.

The most conclusive evidence of symbiotic fixation of nitrogen by alder root nodules has been presented by Bond and his coworkers.[1] These investigators, working with modern techniques, have removed all doubt as to the function of nodulated alder roots in nitrogen fixation. Their work shows that alder root nodules fix nitrogen, that this nitrogen migrates to other parts of the plant, and that the amount of nitrogen so contributed exceeds that supplied by many of the legumes. This research was done with *Alnus glutinosa*, but similar nitrogen-fixing properties have been shown by root nodules of *A. rubra* collected in Oregon. A suspension prepared by crushing these nodules in water was applied to the roots of seedlings of *A. glutinosa*, which subsequently developed nodules. Control plants, not inoculated, did not form nodules. Superior growth of inoculated plants indicated that nitrogen-fixation was proceeding normally in the nodules. It thus appears that the *A. rubra* organism is as effective as that of *A. glutinosa*, even though not identical.[2]

[1]Bond 1955, 1956, 1957; Bond *et al.* 1954; Bond and MacConnell 1955; Bond and Scott 1955.

Description and History of the Study Area

Site of this study is an area along the western boundary of the Wind River Experimental Forest in southwestern Washington. This part of the experimental forest occupies a long, north-facing slope that was swept by a series of disastrous fires, starting with the historic Yacolt fire of 1902.

The soil is a well-drained silty clay loam. Parent material is of an igneous source, including basalt, andesite, and breccias. With a few localized exceptions, soil depth exceeds 5 feet. Slopes range from 0 to 60 percent presenting aspects from north to southeast. Average annual precipitation is about 90 inches.

In 1929, the area was planted to Douglas-fir at an 8- by 8-foot spacing. In May 1933, a strip through the fir plantation was interplanted with 2-0 red alder seedling as a trial of alder for firebreak purposes. The strip, 72 feet wide, follows a north-south section line for most of its 1-mile length, generally at right angles to the contour of the land.

Seed for the alder stock was gathered near Olympia, Washington, about 100

[2]From personal correspondence with G. Bond, Oct. 31, 1957.

miles north of Wind River at an elevation of 50 feet above sea level. It is important to keep in mind that stock of this low-elevation source was planted on the study area at an elevation of 2,000 feet, where early examinations indicated severe frost damage to the young alder seedlings. Very likely other abnormally cold periods (Duffield 1956, Daubenmire 1957) also inflicted damage on this alder plantation.

Experimental Methods

A series of paired 1/20-acre plots was established in the fall of 1956. Each pair consisted of a plot in the center of the fir-alder strip and another 2 chains west, outside the alder influence. Plots were rectangular (33 feet by 66 feet), and 12 pairs were installed at a spacing of 2 chains.

Because the plantation was not designed originally for this study, it was necessary to assume within-block randomization to provide a basis for testing treatment differences. While this does not fully meet the requirements for true randomization, it was considered preferable to the alternative of forgoing any test of significance. This assumption was further considered reasonable because the study extended for a half mile along a section line which traversed a wide range of slope, aspect, and soil conditions.

On each plot, d.b.h. was recorded for all trees measuring 2.6 inches or more. Heights were determined for the two largest-, two smallest-, and two median-d.b.h. trees. All trees measured were planted Douglas-fir or alder. No naturally seeded trees were found, except a very few small seedlings of Douglas-fir and western hemlock (*Tsuga heterophylla* (Raf.) Sarg.)

Within a radius of 30 feet from a point one chain south of each plot, the two largest dominant Douglas-firs were felled. For each of these trees, height and d.i.b. at breast height were measured at 5-year growth intervals. Measurement for form class determination was also completed. All needles from all limbs in the third whorl from the tip of the tree were taken for foliage nutrient analysis, and length of limbs in this whorl was recorded.

Soil samples extending 3 inches immediately beneath the fresh litter were taken in 350-cc metal cylinders. One such sample was collected at every 10-foot interval along a diagonal of each plot. These individual samples were then composited for each plot for chemical and microbiological analysis.[3]

All soil and foliage samples were taken during the last week in September.

Results

Site quality. Measurements of dominant firs converted to average height of dominants and codominants (Staebler 1948) indicated the study area to be site index 110 (midclass IV) for Douglas-fir (McArdle *et al.* 1949). Natural fir stands of comparable age on other parts of the experimental forest indicate about the same site.

Stand growth. Douglas-fir mixed with alder in comparison with Douglas-fir growing alone (Fig. 1) showed no real difference in either height or diameter (Table 1). There were significantly fewer fir stems in the fir-alder mixture than in the pure fir plantation, however, and the basal area of fir in mixture was correspondingly less than that of fir grown alone. This last is attributed to competition from the alder component, which averaged 59 percent of the total stems in the mixed stand. Despite fewer fir stems in the mixture, however, stocking was still adequate, averaging 443 fir stems per acre. Volume of the fir component of the mixed stand was 209 cubic feet per acre less than the volume of the pure fir stand.

Although main concern in stand growth centered on the fir component, it is of in-

[3]Soil and foliage nutrient analyses were made by the Oregon State Soil Testing Laboratory, Oregon State College, Corvallis, Oreg. Microbiological analyses were made by Dr. K. C. Lu, Department of Bacteriology, Oregon State College.

FIGURE 1. *Pure Douglas-fir (A) and alder-fir (B) plantations. Differences in crown closure and density of understory vegetation are typical of the entire study area.*

terest that when fir and alder measurements are combined, more than twice the cubic volume of wood was produced in the mixed stand than in the pure Douglas-fir stand. Despite much greater competition, average diameter of the Douglas-fir in the mixed stand was not greatly different from that in the pure plantation. Ap-

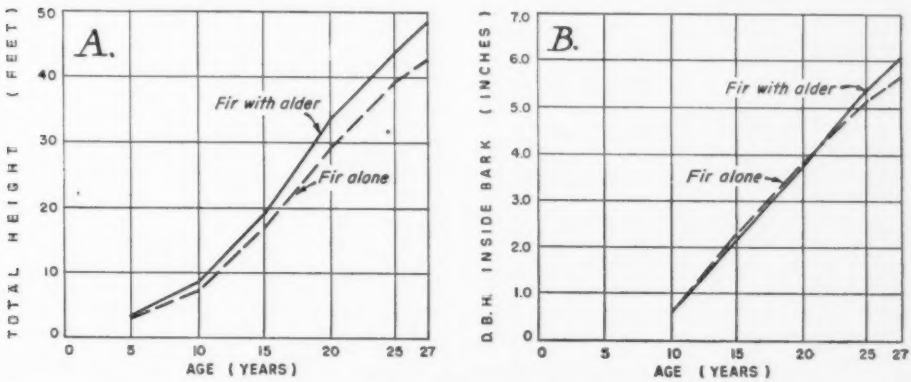

FIGURE 2. *Periodic growth of dominant Douglas-fir (basis, 48 trees). A, The difference in rate of height growth during the period 25-27 years is significant at the 5-percent level. B, The difference in rate of diameter growth during the period 20-25 years is significant at the 5-percent level; the difference during the period 25-27 years is significant at the 1-percent level.*

parently, at the 8- by 8-foot spacing of the Douglas-fir plantation, much of the productive capacity of the site has been unused during the first 27 years of growth. This assumption is supported by results of a nearby Douglas-fir spacing study. In a comparison of spacings ranging from 4 by 4 feet to 12 by 12 feet, stands planted at the wider spacing did not produce as great a cubic volume until after 20 years (Eversole 1955).

Growth of dominant Douglas-fir. Slight diameter and height differences in favor of the mixed stand were found for dominant firs on the study plots and for dominants felled between plots (Table 2). In no case, however, were these differences sufficiently strong to be statistically real except for height of felled dominants. There, a height advantage of 5.6 feet for fir in mixture with alder proved significant.

A stronger indication of growth differences between the mixed and pure stands was gained from a stem analysis of felled dominants (Fig. 2). This showed that for the past few years dominants in the mixed stand had been growing at a faster rate than those in the pure fir stand. Throughout the life of the mixed plantation, average height of dominant fir has been greater than that of fir growing alone. The difference, however, was never enough to be statistically real until age period 25-27 years, when it widened definitely in favor of fir growing with alder.

Average rate of diameter growth did not differ appreciably between the two conditions during the first 20 years of growth. However, during the age period 20-25 years the diameter growth rate of fir with alder assumed superiority over that of fir alone. This difference again increased appreciably during the next 2-year period, age 25-27 years.

TABLE 1. Average stand characteristics for trees with d.b.h. of 2.6 inches or greater at age 27 years.

Item	Unit of measure	Douglas-fir			Red alder (mixed with Douglas-fir)
		Mixed with alder	Pure stand	F[1]	
Height:	Feet				
Average[2]		33.87	32.78	0.62	36.12
Tree corresponding to tree of average basal area		31.9	32.2	.....	37.3
D.b.h. (o.b.):	Inches				
Average of all trees measured		4.57	4.48	0.73	4.53
Tree corresponding to tree of average basal area[3]		4.71	4.60	0.99	5.29
Stems per acre	Number	443	568	16.84	627
Basal area per acre	Square feet	53	66	6.46	75
Volume[4] per acre	Cubic feet	894	1,103	4.38	1,464

[1]Test of significance of difference between fir in mixture and fir growing alone. Value of "F" required for significance: at 5-percent level, 4.84; at 1-percent level, 9.65.

[2]Obtained by averaging heights of two trees of largest d.b.h., and two trees of median d.b.h. on each plot, by treatment.

[3]Obtained from curve constructed by combining all height data for each treatment.

[4]Total stem, including stump and tip.

TABLE 2. Average height and diameter at age 27 years: dominant Douglas-fir in mixture with red alder and dominant Douglas-fir in a pure stand.

Item	Unit of measure	Douglas-fir: Mixed with red alder	Douglas-fir: Pure stand	F[1]
Plot dominants:				
D.b.h. (o.b.)	Inches	6.97	6.52	1.62
Height	Feet	45.17	42.79	.80
Felled dominants:				
D.b.h. (o.b.)	Inches	6.80	6.47	.88
Height	Feet	48.62	42.95	5.41

[1]Test of significance of difference between fir mixed with alder and fir in a pure stand. Value of "F" required for significance at the 5-percent level of confidence is 4.84.

Form class and limb length. To determine the effect of greater density in the mixed stand, form class of Douglas-fir was determined as:

$$\frac{\text{d.i.b. at top of first 16-foot log}}{\text{d.b.h. (o.b.)}} \times 100$$

This measurement, which was made on all felled dominants, proved significantly higher for fir grown with alder.

Length of limbs in the third whorl from the tip was also significantly greater for fir in the mixed stand. This is considered to indicate generally a broader, more vigorous upper crown for fir grown with alder. The following tabulation shows averages of these measurements:

	Limb length (inches)	*Form class (percent)*
Douglas-fir with alder	43.5	74
Douglas-fir—pure stand	31.1	67
F	15.18	8.63

Values of F required for significance may be found in Table 1.

Soil and foliage nutrient status. Beneath the alder-fir mixture, total soil nitrogen was 65 percent greater than that beneath the pure fir stand (Table 3). Even in the pure fir stand, however, soil nitrogen content exceeded values established as indicators of low nitrogen status (Forest Soils Committee of the Douglas-fir Region 1957).

In turn, the greater soil nitrogen supply beneath the mixed stand was reflected in results of analyses that showed fir growing with alder had significantly more foliar nitrogen than did fir growing alone (Table

TABLE 3. Average values for chemical properties of soil and foliage in a 27-year-old stand: Douglas-fir in mixture with red alder and Douglas-fir in a pure stand.

Property	Unit of measure	Douglas-fir: Mixed with red alder	Douglas-fir: Pure stand	F[1]
Total nitrogen:				
Soil	Percent	0.23	0.14	10.51
Foliage	Percent	1.27	1.20	5.44
Phosphorus:				
Soil	Ppm	11	11	1.41
Foliage	Percent	.14	.18	17.20
Potassium:				
Soil	Ppm	212	197	.46
Foliage	Percent	.95	.99	1.05
Calcium:				
Soil	Ppm	666	496	2.02
Foliage	Percent	.46	.46	----
Magnesium:				
Soil	Ppm	192	155	1.94
Foliage	Percent	.24	.32	8.06
Soil reaction	pH	5.50	5.60	2.81
Cation exchange capacity:				
Soil	me/100 g	26.10	23.60	1.99

[1]Test of significance of difference between fir mixed with alder and fir in a pure stand. Value of "F" required for significance: at 5-percent level, 4.84; at 1-percent level, 9.65.

3). On the other hand, foliar content of phosphorus and magnesium was greater in the case of fir grown without alder, although soil content of these two elements did not differ between treatments. This latter finding could be attributed to the so-called "dilution effect" in that a comparatively small total amount of phosphorus and magnesium must be distributed on a larger amount of living tissue in the mixed plantation where cubic volume of fir plus alder was more than twice that of the pure fir stand (Table 1).

Potassium and calcium content of soil and foliage was not different between treatments, nor were soil reaction and cation exchange capacity.

A number of studies have produced evidence that nutrient concentration in older needles is less than in current foliage. However, any possible reduction in nutrient content caused by compositing current and past two years' needles, as was done in this study, was not sufficient to prevent demonstration of significant differences in nitrogen content between treatments.

Numbers of soil micro-organisms. There was apparently no real difference in number of bacteria or actinomycetes, nor was the ratio of the two groups different between stands sampled (Table 4). Fungi, however, were more numerous in soils beneath the pure fir plantation.

An explanation for the difference in fungal population of the two stands is not readily apparent since the study dealt only with total numbers. The findings are offered, however, as a possible starting point for a more intensive investigation.

Table 4. Average numbers of soil micro-organisms in a 27-year-old stand: Douglas-fir in mixture with red alder and Douglas-fir in a pure stand.

Group	Douglas-fir		F[1]
	Mixed with red alder	Pure stand	
Bacteria	1,500	1,100	2,71
Actinomycetes	336	223	.57
Fungi	39	56	13.80
Ratio: Bacteria to actinomycetes	4.7	5.4	0.82

[1]Test of significance of difference between fir mixed with alder and fir in a pure stand. Value of "F" required for significance: at 5-percent level, 4.84; at 1-percent level, 9.65.

Summary and Conclusions

A study was made of a 27-year-old mixed Douglas-fir and red alder plantation on the Wind River Experimental Forest in southwestern Washington. This plantation differs from natural mixtures of fir and alder commonly found in the Douglas-fir region in that genetic unsuitability of the alder planting stock has led to periodic cold damage, which has curtailed its growth. Thus, the Douglas-fir has been able to compete more strongly than it could in a natural mixture, where red alder usually dominates the site during early years of growth.

Major findings of the study were:

1. Although there were more Douglas-fir stems in the pure plantation, there yet remained in the mixed stand an average of 443 stems per acre, which is considered satisfactory stocking. In addition, there were 627 alder stems of about the same average diameter and height as the firs. More than twice the total cubic volume of wood was produced in the mixed stand, with no adverse effect on average size of trees.
2. Dominant firs in the mixed stand showed significantly greater average diameter growth than those in the pure stand for the age periods 20-25 and 25-27 years. Measurements between ages 25 and 27 years indicated that these same dominants were also growing in height at a faster rate than those in the pure stand.
3. Form class of fir grown with alder was higher than that of fir grown alone. Also, limb measurements indicated a generally broader, more vigorous upper crown in the fir grown with alder.
4. Total nitrogen content, both of the soil

and of Douglas-fir foliage, was significantly greater in the plantation having alder in mixture.

5. Numbers of soil bacteria and actinomycetes, and their ratio did not differ significantly between the two conditions sampled. Fungi, however, were more numerous in soil beneath the pure fir stand.

Admixture of red alder in this Douglas-fir plantation evidently has contributed to increased growth of dominant firs, beginning at about age 20 years. This attests further to the reputed soil-improving quality of red alder through symbiotic fixation of nitrogen in root nodules.

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Hila of Full and Empty Longleaf Pine Seeds are Distinguishable

Note by B. F. McLemore

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Full and empty seeds of most longleaf pine trees (*Pinus palustris* Mill.) can be separated with a high degree of reliability by examining the hila. In this species the hilum, which marks the place where the seed was attached to the cone scale, is large enough to observe without a hand lens. It is located where the wing is joined to the seed. In all but a very few longleaf pine trees, seeds having a distinct hilum are full, while those with a faint scar are empty. Figure 1 shows the difference in prominence of the hilum on full and empty seeds from a single tree.

Longleaf seeds are too buoyant for sorting by water-alcohol flotation, while gravity tables, blowers, and other conventional equipment work well only with fairly large quantities. When cutting tests cannot be made and when time or equipment is lacking for determinations with X-rays or balances, the method described here may be useful for small lots, such as frequently result from tree-breeding experiments.

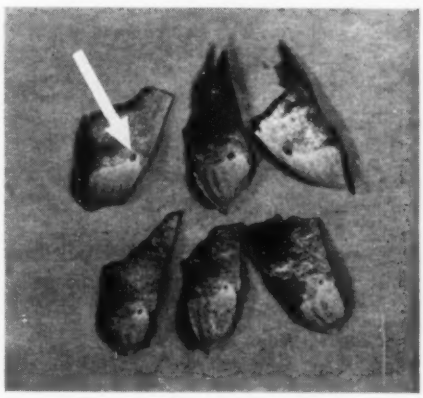

FIGURE 1. *The three longleaf seeds at top have distinct hila and are full; those at bottom have indistinct hila and are empty (hilum of first seed is indicated by arrow).*

The effectiveness of the technique was verified by separating 1,993 seeds, representing 14 different trees, into 1,393 "full" seeds and 600 "empty," on the appearance of the hila alone. Cutting tests showed that 97 percent of the determinations had been correct. In one aberrant tree, determinations were 83 percent correct; in all others they were at least 95 percent correct and in 6 instances they were perfect.

Three precautions should be observed. First, only seeds with wings or wing stubs still attached should be examined, as the hilum is obscured if the entire wing is removed. This requirement is no great drawback, because longleaf wing stubs almost never become detached. Second, seed from different trees should be kept separate; otherwise, tree-to-tree variations in color and size of seed and in character of the hilum reduce the reliability of the technique. Third, in an occasional longleaf pine ill-defined hila may reduce the accuracy of determinations. In such instances, errors will have to be accepted, or full and empty seeds will have to be separated by X-rays or by weighing.

Intraspecific Root Grafting and the Survival of Eastern White Pine Stumps

BY
F. H. BORMANN

ROOT GRAFTING is common among eastern white pine (*Pinus strobus* L.) trees over the whole range of soil conditions tolerated by the species (Bormann and Graham 1959). Such grafts are functional in translocation and provide the means by which dominant trees in a grated clump eventually "adopt" the roots of suppressed trees whose tops die down to the stump level (Bormann 1959, 1960; Bormann and Graham 1959; Graham 1960). Living stumps resulting from this natural process are common in many eastern white pine stands.

Relatively little is known of the behavior of the stumps of trees cut during forestry operations. A preliminary study indicated that many white pine stumps remained alive during the first growing season after cutting, but it was impossible to judge whether they did so solely because they were grafted to intact trees or whether stumps not so grafted had a limited potential to remain alive.

To obtain information on longevity after cutting, general anatomical condition, and the relative mitotic activity of lateral meristems, a comparative study was undertaken of stumps grafted to intact trees and those not grafted to intact trees. (Hereafter, these will be referred to as grafted and non-grafted stumps.) It was hoped that this study might also yield additional information on the mechanics and physiology of root grafting, and point out some practical considerations for foresters.

Methods

Since excavation of root systems was impractical, it was necessary to devise ways in which non-grafted stumps could be separated from grafted stumps. The former could be rather easily found by studying stumps in clearcut stands where all intact trees had been removed. This was done in 11 stands which had been clearcut at various times. According to common clearcutting practice a few scattered trees remained in each of these stands. To minimize the possibility that any of the stumps were grafted to these trees, only stumps farther than 5m from the nearest intact tree were included in the study. Injection experiments (Bormann and Graham 1959) have shown slight possibility of grafts between white pine trees separated by a distance of 5 m or more.

Eleven partially-cut stands in which trees were removed here and there throughout the stand were also selected for the study. Here the determination of grafted and non-grafted stumps was more difficult. If a stump was dead, it was impossible to make this determination without excavating its root system. For living stumps, however, it was assumed that they were grafted to intact trees if they had remained alive for a period of time exceeding the maximum longevity for non-grafted stumps. Since the study in the clearcut stands indicated that no stumps cut prior to the fall of 1958

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were alive during the growing season of 1959, the partial-cutting phase of the study was limited to stands treated 2 to 10 years prior to the 1959 growing season. Thus it could be assumed that all living stumps found in these stands were grafted to intact trees—a view that is further substantiated by the following evidence.

(1) Nine of the 58 stumps found to be living were partially excavated and observed to be grafted to an intact tree. (2) The writer has noted in living stumps known to be grafted to intact trees that the cambium below the cut often produces a wound callus. A similar phenomenon has been reported in stumps of Norway spruce, *Picea abies* (L.) Karst., grafted to intact trees (Wichmann 1925). Twenty nine of the 58 living stumps in the partially-cut stands exhibited callus growth of this type. (3) Ten stumps found to be grafted to intact trees by Bormann and Graham (1959) were carefully examined one year after cutting of the trees and injection of the stumps with dyes or radioisotopes. All were found to be alive. Eight stumps, treated in the same manner and found to be free of grafts, were dead one year later. For the present study, this suggests that living stumps of trees cut one or more years previously, are root grafted to intact trees. (4) Bormann and Graham (1959) using radioisotope tracers and excavation, found that 7 out of 7 naturally occurring living stumps were grafted to intact trees.

For the most part, the stands, all of which occurred within a 20-mile radius of Hanover, New Hampshire, were found on hillsides with soils of varying texture. Of the 22 stands, 20 had seeded in naturally on abandoned pastures, while two were plantations.

A single 20 x 20 m quadrat was laid out in each stand. In clearcut stands an effort was made to place the quadrat where there were relatively few standing trees, while in partially-cut stands an effort was made to avoid local clearcut areas. Within the quadrat, all white pine stumps were studied. For each stump, an estimate was made of the degree to which it was shaded by slash. Its age was determined by a ring count and its diameter was measured with calipers. The top of the stump was then divided into four quadrants, N, W, S, and E, the bark was peeled down to the roots, and a visual estimate was made of the percentage of living tissue in each. Living tissue was identified by a white, glistening, and healthy appearance of the sapwood and inner bark exposed by peeling. When the tissue of the inner bark had a pinkish, watersoaked appearance, apparently transitional between healthy and dead tissue, it was not included in the estimate.

Some stumps had living tissue around their entire circumference. In most stumps however, living tissue occurred as vertical streaks of varying widths extending into the roots. Generally the living tissue did not extend up to the cut surface of the stump, but stopped several inches below it.

The anatomical condition of the cambial zone of selected stumps was studied by observing sections made from blocks removed from living tissues of the stump. Blocks including intact xylem, cambium, and phloem were obtained by making two parallel saw cuts and chipping out the intervening section. The blocks were then wrapped in wet paper towels, placed in polyethylene bags, and stored at 4°C until they were sectioned and examined several hours later. The cambial zone of each block was studied by microscopic observation of freehand sections made in both transverse and radial longitudinal directions. Since all stumps examined had been the result of cutting in the dormant season, the large ring of xylem formed during the last growing season of the intact tree formed a convenient surface of reference.

The diameter, compass bearing, and distance from the stump were recorded for the two nearest intact trees. A previous study (Bormann and Graham 1959) indicated that these were the trees most likely to be grafted to the stump. Similar measurements were made for the two

TABLE 1. Clearcut stands. Number of stumps alive or dead in July and August of 1959 in relation to time of cutting.

Age of tree at time of cutting. (Yrs.)	Time of cutting: Mar.-Apr. 1959 (1 stand)		Sept. 1958-Feb. 1959 (4 stands)		Winter 57-58 (5 stands)		Summer 1957 (1 stand)	
	Alive	Dead	Alive	Dead	Alive	Dead	Alive	Dead
0-19	0	0	0	0	0	0	0	1
20-39	1	1	0	8	0	17	0	1
40-59	20	1	1	32	0	31	0	13
60-79	0	0	0	5	0	32	0	5
80-99	0	0	0	0	0	7	0	0
Total	21	2	1	45	0	87	0	20

nearest stumps.

Many of the recently cut stumps were being attacked by larvae of the Pales weevil, *Hylobius pales*, and other pests. Fungus infections, such as blue stain, were also common.

Results and Discussion

Stumps not grafted to intact trees. Of the 176 non-grafted stumps occurring in clearcut stands only 22 were alive when examined in July and August of 1959 and 21 of these occurred in a single stand cut in March and April of 1959 just preceding the onset of the growing season (Table 1). Only 1 of the 46 stumps resulting from the 1958-59 fall and winter cutting was alive, while all of the 107 stumps from the winter cutting of 1957-58 and earlier were dead. Subsequent observations of the stand cut in March and April of 1959 indicated that the living stumps were rapidly deteriorating in late August of 1959 and that none was alive in the summer of 1960.

These results indicate that non-grafted stumps of cut trees may survive part or all of the growing season following the cutting. Apparently the time of cutting has a considerable influence on the stump's survival during the following growing season. Many of the stumps cut in the early spring survived a large part of the growing season, while only one of those stumps from cutting made from October to February was alive and healthy at the middle of the growing season. This suggests that winter conditions were deleterious to the survival of these stumps. There was also some indication that stumps shaded by slash were able to stay alive longer.

In view of the possibility that some of these stumps may have made some radial growth, sections from 11 living stumps ranging in age from 32 to 55 years and in diameter from 20 to 65 cm were examined in late July and early August of 1959.

In all sections the cambial zone, composed of several narrow (radial dimension) cells, was adjacent to the 1958 summerwood indicating that the cambium was not mitotically active during 1959. Thimann and Kaufman (1958) have shown that cyclosis is easily observed in cambial sections removed from logs stored at 3 to 4°C. Cyclosis was observed in only one stump section, but cyclosis may have been more common had the sections been taken earlier in the growing season. In one instance numerous starch grains were noted.

Some of these stumps would seem to have had the necessary potential for some cambial division. Their peeled tissues appeared to be as white and healthy as similar tissues peeled from intact trees, and the occurrence of cyclosis and the presence of starch grains in at least one stump suggests that deficiencies of food did not inhibit cambial activity.

Since it is widely accepted that auxin produced by expanding buds initiates cam-

bial activity in the spring a plausible explanation for the lack of cambial activity in these stumps is that auxin, in sufficient quantity to cause initiation, was lacking due to removal of the tops. Wareing (1951) has suggested that the mechanism of cambial activity in eastern white pine is similar to that in ring porous trees, in which he has demonstrated that a slight development of adventitious buds in excised logs is sufficient to initiate some mitotic activity. Since white pine rarely sprouts, auxin produced by adventitious or other buds could not cause cambial initiation in the stump. It is hoped that experiments with auxin implantations in stumps and in excised logs will shed more light on this problem.

The cambial zone graded into larger cells which fitted Abbe and Crafts' (1939) description of young and mature sieve cells. Some cells appeared to be in the bulging stage, while others toward the outside were fully matured, showing well developed callose formation. Sieve areas similar to those shown in Figure 30 of Abbe and Crafts (1939) were observed from 5 to 17 cells removed from the summerwood. They also show that in the intact tree, undifferentiated sieve cells, produced through cambial divisions in the autumn of the previous season, differentiate in the following spring. In the present study, observations on non-grafted stumps, suggest that at least some of the sieve cells laid down at the close of the 1958 growing season had differentiated and matured in the spring and summer of 1959. However, more careful study is required before any general conclusions can be drawn regarding the anatomical condition of the phloem transport system in non-grafted stumps.

Stumps grafted to intact trees. In 9 out of the 11 partially-cut stands 3 to 44 percent of the stumps examined were found to be alive. Living stumps were found in stands cut in the various seasons and in stands cut as long as ten years previously (Table 2). Of the stumps of trees less than 19 years old at the time of cutting, relatively few, 6 percent, were found to be alive, while 28 percent of the 209 stumps of trees cut between the ages of 20 and 59 years were alive. Most of these living stumps were within 2.5 meters of the nearest living tree, with only four having the nearest living trees more distant than 2.5 meters. The maximum distance between a living stump and the nearest living tree was 3.1 m. Eleven stumps, not included in Table 2, farther than 5.0 m from the nearest tree, were dead.

It should be noted that the number of living stumps in partially-cut stands does not provide an exact estimate of the percentage with grafts. It seems likely that some grafted stumps are killed by the action of pathogens and/or insects, or that all members of a grafted clump may be cut with the result that all the stumps die. In either instance, the dead stumps would be mistaken for non-grafted trees.

To determine if radial growth had occurred in these stumps, blocks were removed from six trees, cut in the winter of 1957-58, ranging in age from 33 to 36 years and in diameter from 28 to 37 cm. Cambial activity was confirmed by the presence of small annual increments of xylem and phloem deposited each year since cutting. Often, however, a complete annual ring was not formed because only a portion of the circumference of the stump was living.

Microscopic examination of several of these stumps indicated that the orientation of xylem and phloem cells, immediately below the cut surface, changed considerably after the tree was cut. In one instance, the orientation of the vascular tissues had shifted 180° in two years. The long axes of tissues produced during the growing season of 1957, while the tree was intact were vertically oriented, while those produced during the first season of stump growth were at first vertically but later horizontally oriented. Those produced in 1959 were completely horizontal (Fig. 1). In some peeled stumps, the shift in orientation of cambium was revealed by the ap-

pearance of swirl-like patterns in the grain of the exposed wood. Usually this phenomenon occurred only in the uppermost few inches of the living tissue. These results suggest that factors controlling the orientation of the cambium and its derivatives were severely altered by detopping.

Although some stumps were alive and vigorous throughout their circumference, many had living tissue only in certain quadrants. To determine whether the living portion of the stump was correlated with a particular compass bearing, for example the cooler north side, the distribution of living tissue in all stumps was tabulated by quadrants. Living tissue occurred in 40 N, 40 W, 39 S and 39 E quadrants. An average of 67, 66, 72 and 66 percent

TABLE 2. Partially-cut stands. Number of stumps alive or dead in August of 1959 in relation to the distance of the nearest living tree and the time of cutting.[1]

Age of tree at time of cutting (yrs)	Distance to the nearest tree in meters 0—2.5		2.6—5.0		0—2.5		2.6—5.0	
	Alive	Dead	Alive	Dead	Alive	Dead	Alive	Dead
	SUMMER 1958 (2)[2]				WINTER 1957-58 (2)[2]			
0-19	0	3	0	0	0	1	0	0
20-39	13[3]	22	0	0	6	16	0	8
40-59	11[3]	21	2[3]	2	1	3	0	4
60-79	0	0	0	0	0	1	0	0
Total	24	46	2	2	7	21	0	12
	SUMMER 1957 (1)[2]				WINTER 1955-56 (1)[2]			
0-19	0	0	0	0	1	0	0	0
20-39	5	3	0	2	0	1	0	2
40-59	3	5	0	3	1	1	2	0
60-79	0	0	0	0	0	0	0	1
Total	8	8	0	5	2	2	2	3
	WINTER 1954-55 (1)[2]				SUMMER 1954 (1)[2]			
0-19	1[3]	5	0	0	0	0	0	0
20-39	0	7	0	3	3[4]	0	0	1
40-59	2[3]	9	0	2	1[4]	1	0	4
60-79	0	0	0	0	0	1	0	1
Total	3	21	0	5	4	2	0	6
	WINTER 1953-54 (2)[2]				WINTER 1949-50 (1)[2]			
0-19	1	35	0	0	0	0	0	0
20-39	0	9	0	4	3[4]	4	0	2
40-59	0	6	0	2	2[4]	3	0	4
60-79	0	2	0	0	0	0	0	0
Total	1	52	0	6	5	7	0	6
			SUMMARY 1949-58 (11)[2]					
0-19			3	44	0	0		
20-39			30	62	0	22		
40-59			21	49	4	21		
60-79			0	4	0	2		
Total			54	159	4	45		

[1]Does not include 11 dead stumps greater than 5 m distance from nearest tree.
[2]Number of stands.
[3]Grafts verified by the presence of callus.
[4]Grafts verified by excavation.

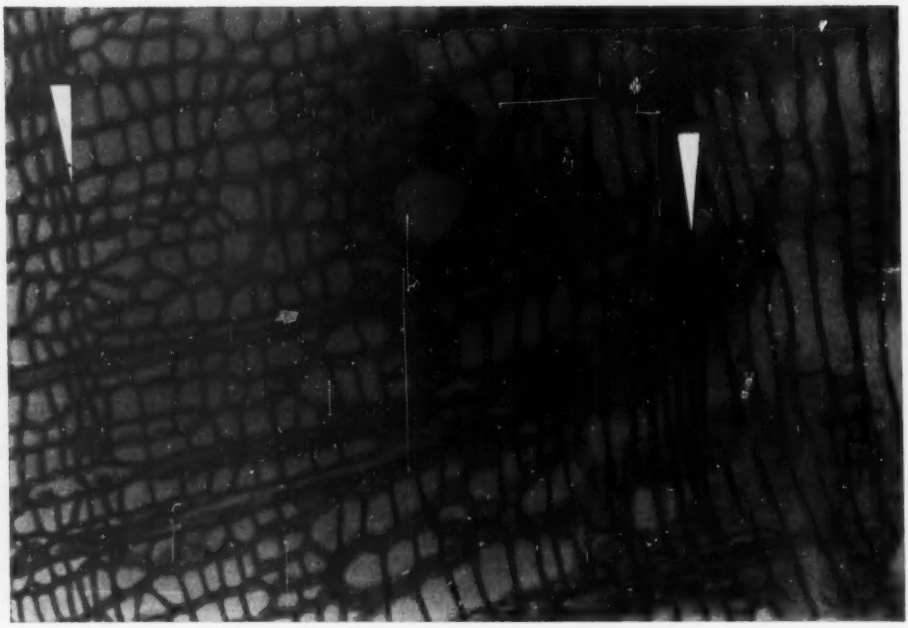

FIGURE 1. *Photomicrograph of a portion of the xylem taken from near the top of a grafted stump. The area between the two arrows represents the 1958 growth. The area to the left of the 1958 growth is 1957 growth while that to theright is 1959 growth. Note how the long axes of the cells have become progressively reoriented since the tree was cut in the winter of 1957-58.*

TABLE 3. Position of closest (compass bearing, not distance) intact tree in relation to the position of stump quadrants with living tissue. All intact trees within 3.2 m distance of stump.

Position of closest intact tree by octant(s)	Degrees of perimeter included in octant(s)	No. quadrants with closest intact tree in octant(s)	Percent of quadrants	Cumulative percent of quadrants
0—Octant same bearing as quadrant	45	48	30.4	30.4
1—One octant to the right or left of zero octant	90	55	34.8	65.2
2—Two octants to the right or left of zero octant	90	46	29.1	94.3
3—Three octants to the right or left of zero octant	90	7	4.4	98.7
4—Four octants from zero octant	45	2	1.3	100.0
Totals	360	158	100.0	

of the tissue was alive in the N, W, S, and E quadrants, respectively. The more-or-less even distribution of living tissue throughout the various quadrants suggests that environmental conditions associated with aspect had little influence on the longevity of the stump.

Observations on the living bases of seemingly dead trees and on living stumps left over from injection experiments (Bormann and Graham 1959) suggested that living tissue often is restricted to that side of the stump nearest to the tree to which it is grafted. Using data from the partially-cut stands it was possible to determine the relationship of the position of living tissue to the position of the two nearest intact trees to one or both of which the stump was most likely to be grafted.

During the field observations, each stump was divided into four quadrants (N, W, S, and E) and the amount of living tissue in each was estimated. At the same time, the compass bearing (N, NW, W, SW, S, SE, E, NE) and distance of the two nearest trees was taken. The area around the stump may be visualized as being composed of eight octants with the two nearest trees occurring in one or two of these octants.

Each of the 158 quadrants with living tissue was considered separately and scored 0 to 4. If a tree occurred in the octant with the same bearing as the quadrant, the quadrant was scored 0; if the closest (compass bearing, not distance) tree occurred in either of the first octant to the right or to the left of the zero octant the quadrant was scored 1; if the closest tree occurred in the second octant to the right or left the quadrant was scored 2; if the closest tree occurred in the third octant to the right or left the quadrant was scored 3; and finally if the closest tree occurred in the octant with a compass bearing opposite to that of the quadrant, the quadrant was scored 4.

To restrict consideration to those intact trees most likely to be grafted to the stumps, only those trees occurring within 3.2 meters of the stump were used. Seventy percent of the trees used in the scoring were within 2 m of the stump, 28 percent were between 2 and 3 m from the stump, and 2 percent were 3 to 3.2 m away. The results of the scoring are presented in Table 3.

Ninety-four percent of the quadrants had the closest tree located in the five octants surrounding the quadrant, while only 6 percent had the closest tree in the three octants on the opposite side. To determine the statistical validity of these data, it was assumed that the occurrence of living tissue in the quadrants was in no way related to the position of the two nearest trees and the probability with which scores 0 to 2 and 3 and 4 were expected to occur was determined. From this, the numbers of living quadrants expected to fall into the two groups of scores was calculated and a Chi-square test was performed. The Chi-square calculated was found to have a probability smaller than 1 percent suggesting that the occurrence of living tissue is not independent of the position of the two nearest trees.

Most of the three and four scores recorded in Table 3 came from recently cut stumps alive in all four quadrants with the two nearest trees localized in one or in two adjacent octants. When these stumps are excluded from the calculations the relationship of the living quadrants to the closest tree apparently becomes more strict. When stumps with only three or less living quadrants are considered, 96 percent of the closest trees are in the five surrounding octants. When stumps with only two or less living quarters are used 100 percent of the closest trees are in the five surrounding octants

Although these data have some weaknesses, for example, only the two nearest trees are used, they support the view that living tissue occurs primarily on that side of the stump adjacent to a tree to which its roots are grafted. They also suggest that this relationship becomes more pronounced as the time since cutting increases.

The restriction of living tissue to that

side of the stump adjacent to a tree to which it is grafted may be explained by two observations.

First, the roots of a tree have little opportunity of coming into contact with a root emanating from the opposite side of an adjacent tree. The trunk of a pine tree may be visualized as the hub of a wheel with its roots as spokes radiating in all directions (see Fig. 5, Bormann and Graham 1959). For the roots of another tree to effect a graft with one spoke, the tree must be in a position such that its root(s) can come into contact with that spoke fairly close to the hub, or that the spoke can come into contact with its root(s) fairly close to its trunk. Roots from trees on the side of the hub opposite from which the spoke emanates have little opportunity to establish contact with the spoke because they are blocked or deflected in their growth by the base of the hub and the bases of large roots radiating outward from it at more or less right angles to it. Since contact between roots is the first requisite to the formation of grafts, few would be expected between the spoke and roots from the opposite side of an adjacent tree.

Second, living tissue appears to be maintained primarily in that section of the stump over a grafted root. This has been observed frequently in old, naturally occurring living stumps and also in some of the root grafted stumps injected by Bormann and Graham (1959). This suggests that food and other substances translocated in the phloem move in vertical streaks with relatively little lateral transport. Similar streaks have been observed in xylem transport of radioisotopes and dyes (Fraser and Mawson 1953, Bormann and Graham 1959). The frequent occurrence of living tissue around the entire circumference of stumps cut 2 years previously suggests that some lateral transport occurs, while the common occurrence of dead portions in the circumference of older stumps suggests that tissue supported by lateral transport may be among the first to die.

The very limited lateral transport within the vascular tissues of the stump has important physiological implications for the intact tree. It implies that the intact tree cannot, through a single graft, utilize the entire root system of the stump for the absorption of water and minerals. Utilization seems to be limited to grafted stump roots and their tributaries.

Biological Implications and Summary

Data presented indicate that stumps of cut white pine trees not grafted to intact trees (they may be grafted to other stumps) are able to stay alive for only the first growing season following cutting. The time of cutting seems to have a direct bearing on the length of time such stumps will remain alive. Many of the stumps of trees cut in early spring remained alive for almost the whole growing season while those cut in the fall and winter were almost all dead by the middle of the growing season. This suggests that winter conditions, in some way, reduce the capacity of these stumps to survive the growing season.

An anatomical study of the cambial region of stumps not grafted to intact trees indicated that, although some stumps were healthy with the cambium exhibiting cyclosis and with starch present in the cells, none of these stumps showed any mitotic activity of the cambium during the growing season following cutting. It may be assumed that the cambium failed to become active due to an insufficient supply of auxin resulting from removal of the top.

Stumps known to be grafted to intact trees show cambial activity with the production of new xylem and phloem tissues each year. In 9 partially-cut stands from 3 to 44 percent of the stumps were alive. In one stand partially cut 10 years previously, 25 percent of the stumps were alive, indicating a considerable potential to remain alive.

The maintenance of cambial activity in these grafted stumps leads to certain conclusions regarding the physiology of grafted partners. The first is that cambial activity is initiated in the stump by auxin translo-

cated to it through grafts. Secondly, continued growth of the stump must also be supported by food translocated from the intact tree. Third, it seems likely that prior to cutting exchanges of auxin, food, and water took place between the grafted partners. Fourth, cutting probably alters the pattern of these exchanges of auxins and other materials by bringing about shifts in gradients.

These assumptions lead to the speculation that one tree may affect or even control activities in another tree grafted to it. For example, if the buds of a dominant tree should break first, it might initiate cambial activity in the base of a suppressed tree before its own buds break. An abundance of auxin produced by a dominant tree might also initiate cambial activity in the base of a suppressed tree before the limited amounts of auxin produced by the buds of such a tree could reach its base. Such a phenomenon could be of considerable importance in shaping relationships between grafted trees.

The physiological relationships of stumps to intact trees to which they are grafted are not yet clear. Frequent observations indicate that in many instances only those stump roots which are directly grafted to the intact tree remain alive and apparently functional.

The intact tree may utilize roots of the stump to increase its supply of water and minerals (suggested by Page 1927), or at first, the intact tree may tap the supplies of food stored in the roots of the stump for its own use (Bormann and Graham 1959). Perhaps a combination of these processes, plus a more favorable environment around the crown of the remaining tree, all contribute to the rapid increase in growth of many white pine trees following thinning (Adams 1935).

The incidence of *Fomes annosus*, a root rotting fungus, is becoming increasingly important in thinned stands of white pine (Fowler 1959). This fungus may spread through root grafts or points of contact between non-grafted roots (Anonymous 1960). This indicates that freshly-cut grafted or non-grafted stumps may serve as infection courts for the fungus, but little is known of the relative efficiency of each. The continuity of tissue between the grafted stump and the intact tree would seem to offer an ideal pathway for the spread of this or other root rotting fungi. The fact that fairly large numbers of grafted stumps remain alive for years after removal of the top suggests, however, that many of the grafted stumps have a considerable resistance to fungi or insects.

Thinning with silvicides is becoming important. Recently, however, Bormann and Graham (1960) reported that serious damage to remaining trees can result from the translocation of silvicides through root grafts from the poisoned trees.

The manner in which a stump affects the growth of a tree to which it is grafted, the role of grafted stumps in disease transmission, and the translocation of silvicides between grafted trees would seem to be of prime importance to the forester. It is apparent that considerable basic research on the biological ramifications of intraspecific root grafting is required before meaningful, long range, white pine management programs can be established.

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The Use of Chemicals in Southern Forests

Robert W. McDermid, Editor, Louisiana State University Press, Baton Rouge, Louisiana, x plus 152 pp. illus. 1961. $4.

Review by H. A. Fowells

Forest Service, U. S. Department of Agriculture

If anyone doubts that forestry in the South is reaching a stage of intensive practice, this book should be a convincing argument. Reporting the Ninth Annual Forestry Symposium of the School of Forestry and the General Extension Division of Louisiana State University, this book covers the broad spectrum of the use of chemicals in forestry.

The first of three major sections deals with forest fertilization. Although the hopes of foresters are high for substantial increases in growth from fertilization and there have been isolated dramatic responses, there have been little or no general benefits. There is, however, a general conclusion that much more research is in order.

The second part of the book, devoted to the use of herbicides, discusses basal applications, foliar applications from the ground, and applications by aircraft. The discussion shows plainly the financial advantages of controlling competition by herbicides. But to dampen the over-enthusiastic, a final chapter brings out the hazards and liability aspects of misuse of some of these wonder chemicals.

The last section is concerned with forest protection. The discussion of bombing fires with chemical fire retardants suggests that this novel technique may become the regular "first attack" as protection practices intensify. The possibilities of combatting disease and insects with systemics are intriguing, to say the least, and this method may avoid the conflicts which arise, as discussed in the last chapter, from the widespread spraying of chemicals for direct control.

A much, much bigger book could have been written on this wide range of topics. But this book can serve, as the editor intends, to show that there is progress in the use of chemicals in forestry.

Variations in Total Solar Radiation In Three Norway Spruce Plantations

BY
P. E. VÉZINA

VERY LITTLE is known about the amounts and variations of total solar radiation[1] in forest stands. Yet certain important problems in forestry may be resolved through the measurement of solar radiation intensity under forest conditions. Lack of reproduction may be a result of radiation deficiency at certain hours or seasons. Conversely, too much radiation may favour the development of competing herbs and shrubs to the detriment of the desired species. The stem and crown formation of individual trees, and hence the volume of wood produced, are dependent on solar radiation in the forest. Solar radiation, besides, affects the branching habit of the trees, and especially the position of the leaves. A knowledge of the radiation requirements of various forest trees is indispensable when applying silvicultural treatments. Other silvicultural problems, such as choice of tree species, stand conversion, and underplantings may be solved by an understanding of the maximum and minimum levels of total radiation and of its changes in various well characterized stands. Increased activity in the field of forest photometry has followed improvements in equipment and instruments (Burns 1927, Gast 1930, Shirley 1935 and 1945, Aikman 1936, Wright 1943, Roussel 1953, Courvoisier and Wierzejewski 1954, Logan 1955 and 1959, Evans 1956, Lemmon 1956, Atkins 1957, Dore 1958, Fairbairn 1958, Czarnowski and Slomka 1959, Vézina 1960, and many others).

The Problem

When considering the amounts and variations of light in the forest one is confronted with several questions. How does the character of the stand, the day to day weather, or season of the year affect the amount of light? How does light vary between stands, within a stand, with daily weather, or with the season of the year? What interactions are involved? It seemed worthwhile, therefore, to make a study of the light regimes of diversely thinned stands of a given tree species. This paper is presented for the purposes of (1) acquainting forest research workers with a new model of radiation-integrating pyranometer and (2) presenting original data concerning the transmis-

[1]Light, strictly speaking, refers to that portion of radiant energy composed of waves of frequencies between 0.8 and 0.4 thousandth of a millimeter which is perceived visually. In photometry, however, insolation includes also the invisible infra-red and ultraviolet rays emitted by the sun and sky and having short wavelengths (about 3 and 0.3 microns). These are important both biologically and energetically. *Total solar radiation* includes both visible and invisible rays.

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This paper is a small portion of a dissertation prepared under the guidance of H. Leibundgut and submitted in 1959 to the Graduate School of the Swiss Federal Institute of Technology in partial fulfillment of the requirements for the D.Sc. degree. The author was Canadian National Research Council Scholar in Switzerland, 1957-58. He gratefully acknowledges assistance from A. Linteau and J. D. MacArthur. Manuscript received Sept. 8, 1960.

sion of radiation through the canopy of spruce stands.

The Experiment

In the Demonstration Forest of the Swiss Federal Institute of Technology, near Zurich, three 100-foot-square plots were established in three adjacent pure spruce stands. Plots were selected so that stand and site conditions on each, other than stand density, were as similar as possible (Table 1).

The plots were in 40-year-old even-aged plantations of Norway spruce (*Picea abies* (L.) Karst), a species sometimes planted in eastern Canada and extensively in New England since 1880. The stands had been thinned to three different grades at 6-8 year intervals but had been untouched for 5 years prior to 1958. The understory on two of the three plots was absent. A dense patchy distribution of *Oxalis, Luzula* and other herbs was present on the third plot. Topography was a regular (about 10 percent) middle slope facing northwest and with imperfect surface drainage. The soil in all three plots was classified as a typical brown forest soil developed on a morainic deposit and covered with a shallow layer of *mor* humus.

Sampling Methods

In a characteristic place near the center of each 100-foot-square study plot, under the selected canopies, a wooden post was erected. On this was mounted a PBK-type pyranometer (Courvoisier and Wierzejewski 1954) at the height of 5.4 feet above ground. In order to obtain a reference radiation intensity, another pyranometer was located at the same level in an open area not far away. Pyranometers were calibrated in the field both before and after installation. A previous experiment on sampling variance within the stands, conducted with 8 pyranometers, had shown that spatial variations in radiation intensity under such regular, high canopies of mature conifers are very small, that is, less than one percent (Vézina 1960, p. 89).

TABLE 1. Stand data[1] for the three study plots in spruce type.

Plot	Stems per acre	Volume per acre	Mean height
	No.	*Cu. ft.*	*Ft.*
1	688	8570	52
2	455	5370	52
3	330	5670	54

[1]Based on the 100-foot-square plots.

Instrument

Measurements of total solar radiation were made by means of a new model of Bellani pyranometer[2], an integrating instrument which at a freely exposed point, measures the solar radiation originated by the sun, scattered by the sky or reflected by surroundings and ground. The instrument gives a daily sum of total insolation in calorific units per unit of area of the spherical receiver, i.e., the number of calories reaching a freely exposed sphere with a surface area of one square centimeter.

The pyranometer consists of two concentric glass spheres with an intermediate vacuum. The inner sphere, which is covered by a film of silvered metal, is partially filled with alcohol. A tube of thin glass extends downward from near the top of the inner sphere and projects to a distance of several inches below the outer sphere. The tube is open at its upper, and closed at its lower end and the projecting portion is graduated from 0 to 37.5 cm (Fig. 1).

The greatest part of the solar radiation (except a portion of ultraviolet rays) is absorbed more or less by the inner sphere and its alcohol contents. Then, the sphere and its contents become hot, and tend to

[2]The Bellani pyranometer is the oldest instrument for measuring total solar radiation and is still in use. It was described for the first time in 1836 by its inventor, the Italian physicist P. Angelo Bellani (1776-1852). It was developed and manufactured by the meteorological observatory, Davos, Switzerland, where it is available at the approximate cost of $125 each. It is not sold on a commercial basis.

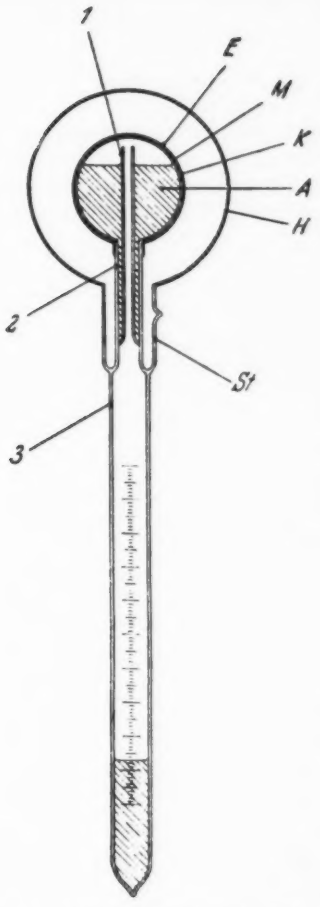

FIGURE 1. *Schematic section through the pyranometer. E = Spherical receiver; M = Metallic cover; K = Glass sphere; A = Alcohol; H = Outer sphere; St = Place of support; 1, 2, 3 = Glass tube (After Courvoisier and Wierzejewski 1954).*

lose their heat, not by conduction or convection, because of the surrounding vacuum, but by radiation of long wavelengths which heats the glass of the outer sphere. This sphere then radiates half towards the exterior, half towards the interior. Consequently there is a concentration of heat on the inner sphere and its contents, and the alcohol evaporates and distills. The distilled alcohol accumulates in the graduated tube which is distinctly colder. The tube is of transparent glass, thinner than that of the spheres, which absorbs less solar radiation. Furthermore, such heat as is absorbed from the sun, and the alcohol, is immediately lost by conduction, convection, and radiation.

Measurements and Analysis

The level of alcohol in the graduated tube may be checked at any time but in this experiment this was normally done only once a day a few moments after sunset. The difference of values of readings on consecutive days, multiplied by a standard factor, give the energy of radiation in gram calories per square centimeter that reached the sphere during the time between the readings. The factor noted in the standard certificate furnished with each instrument is, however, not absolutely constant for all weather conditions. It varies slightly with air temperature, wind velocity, and level of alcohol in the graduated tube. It was therefore necessary to correct the standard factor to the nearest 5°C, using the 40-year monthly normal for Zurich, to ensure an error of daily sums of radiation measured of less than 3 percent (Courvoisier and Wierzejewski 1954). This represents a great improvement in accuracy over that offered by older models of spherical pyranometers.

The Bellani pyranometer is different from the Gunn-Bellani radiation integrator described by Shaw and McComb (1959) mostly by the fact that the later was modified to record radiation on a horizontal surface. It should be pointed out that radiation received by a spherical surface differs from that received by a horizontal surface. The standard network observation is of solar radiation received on a horizontal surface; and it is also expressed in gm cal/sq cm, as is the Bellani reading. The relation between the two would be a matter of simple geometry if all solar radiation came in a direct beam from sun to object;

TABLE 2. Conversion for the pyranometers used.

Instrument	Plot	Factor
		gm cal/sq cm
PBK 58 507	Open area	9.4
PBK 57 524	1	8.4
PBK 58 506	2	8.5
PBK 57 525	3	9.0

but much of it is scattered and so comes from the whole sky, and so brings a different geometrical relation between spherical and horizontal surface. Under a cloudy sky, and under forest canopy, the amount of this scattered solar radiation is a large fraction of the total. So there is no simple relation between the Bellani reading and the usual meteorological measurement of solar radiation.

Total solar radiation was determined pyranometrically on the basis of cubic centimeters of alcohol for periods of a week (from Thursday night to Thursday night) and at a uniform height of 4.5 feet above ground level. These values were converted to gram calories per square centimeter by means of conversion factors based on the International Pyrheliometrical Scale of 1956. The conversion factors, each of them specific for a given instrument, are shown in Table 2.

Total solar radiation was measured in the open during the entire day, regardless of weather conditions, beginning on April 24 and continuing through October 30, 1958. Under the tree canopies, however, measurements were interrupted during nine weeks, that is, from June 20 to August 21, when instruments had to be moved to other experimental areas.

Duration of Bright Sunshine

In April, duration of bright sunshine[3] was 15 percent lower than the normal of 163 hours, and in July it was 9 percent lower than the normal of 247 hours. A deficit of 33 percent was registered in October when sunshine amounted to 72 hours. June sunshine was nearly normal, amounting to 227 hours. Surpluses were registered in May (+ 6 percent), August and September (both + 8 percent). In general, except in April and October, monthly deviations from the normal were relatively small.

[3]Data from the Zurich weather station.

Results

Weekly totals of insolation in the open, and of transmitted radiation through three Norway spruce canopies, each representing a different thinning intensity, were computed. Results expressed in absolute units (gm cal/sq cm) in the open, and in gm cal/sq cm and as a percentage of that recorded in the open for each of the three study plots are given in Table 3. These results are illustrated by Figure 2.

In the sunniest weekly period in the place of observation in 1958, which extended from June 13 to 19, total solar radiation equalled 1972.9 gm cal/sq cm. The least sunny period was observed from October 24 to 30 when total solar radiation amounted to 468.0 gm cal/sq cm. This strong reduction in radiation intensity in the open in October is partly due to haze,

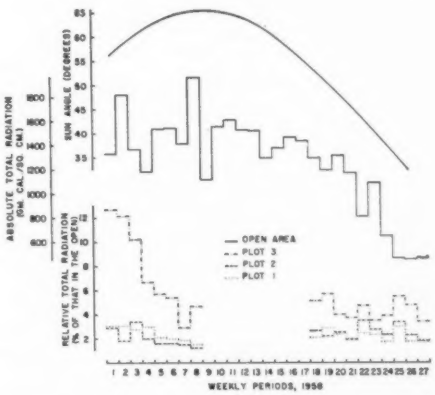

FIGURE 2. *Changes in weekly solar radiation in the open and under Norway spruce canopies compared with astronomical data collected near Zurich, Switzerland.*

TABLE 3. Total absolute (gm cal/sq cm) and relative (percentage of record in the open) solar radiation in the open and transmitted through the crowns of three Norway spruce stands during weekly periods in 1958.

	Weekly periods	In the open	Total solar radiation under spruce canopies					
			Plot 1		Plot 2		Plot 3	
		gm cal /sq cm	*gm cal /sq cm*	*per-cent*	*gm cal /sq cm*	*per cent*	*gm cal /sq cm*	*per-cent*
1	Apr. 25 to May 1	1338.3	41.5	3.1	39.5	2.9	170.0	12.7
2	May 2 to 8	1820.9	55.9	3.1	32.0	1.8	221.8	12.2
3	May 9 to 15	1371.4	38.9	2.8	47.1	3.4	140.1	10.2
4	May 16 to 22	1174.8	35.6	3.0	23.8	2.0	79.2	6.7
5	May 23 to 29	1540.6	33.2	2.2	24.6	1.6	87.9	5.7
6	May 30 to June 5	1545.2	30.8	2.0	24.6	1.6	83.9	5.4
7	June 6 to 12	1416.0	27.5	1.9	21.3	1.5	40.4	2.9
8	June 13 to 19	1972.9	32.4	1.6	25.4	1.3	93.5	4.7
9	June 20 to 26	1115.7						
10	June 27 to July 3	1553.4						
11	July 4 to 10	1611.3						
12	July 11 to 17	1534.9			(Stoppage of 9 weeks:			
13	July 18 to 24	1530.4			Instruments removed			
14	July 25 to 31	1300.5			and replaced)			
15	Aug. 1 to 7	1379.2						
16	Aug. 8 to 14	1472.4						
17	Aug. 15 to 21	1443.5						
18	Aug. 22 to 28	1301.8	28.6	2.2	35.9	2.7	67.0	5.1
19	Aug. 29 to Sept. 4	1195.5	34.8	2.9	27.1	2.3	68.7	5.7
20	Sept. 5 to 11	1335.0	32.4	2.4	32.8	2.5	53.9	4.0
21	Sept. 12 to 18	1171.2	23.1	2.0	22.1	1.9	43.5	3.7
22	Sept. 19 to 25	813.5	20.2	2.5	28.7	3.5	39.1	4.8
23	Sept. 26 to Oct. 2	1091.1	25.9	2.4	29.5	2.7	37.8	3.5
24	Oct. 3 to 9	650.3	11.9	1.8	15.8	2.4	25.5	3.9
25	Oct. 10 to 16	469.9	14.3	3.0	16.2	3.4	26.0	5.5
26	Oct. 17 to 23	456.0	8.2	1.8	10.4	2.3	22.0	4.8
27	Oct. 24 to 30	468.0	9.0	1.9	8.3	1.8	15.8	3.4

as well as to lengthening optical path of sun's rays.

Solar radiation transmitted through the canopies generally showed a decrease from April to October which became more and more marked as the sun angle became smaller in late summer and autumn. This decrease of transmission as noted by Ovington and Madgwick (1955) and more recently by Miller (1959) is probably related also to the growth of spruce needles during the growing season. It is more pronounced in the case of more open stands.

On clear or nearly clear days, transmission of solar radiation was in general lower than on cloudy or overcast days. This trend is revealed in the percentages of radiation transmitted during sunny periods compared with dark or less luminous ones. The trend of clear-day transmission versus cloudy-day transmission is, however, better demonstrated using daily instead of weekly data (Fig. 3). It also provides less chance to disentangle cloud effect from effect of needle growth and change in sun angle with season.

The main reason for this was advanced

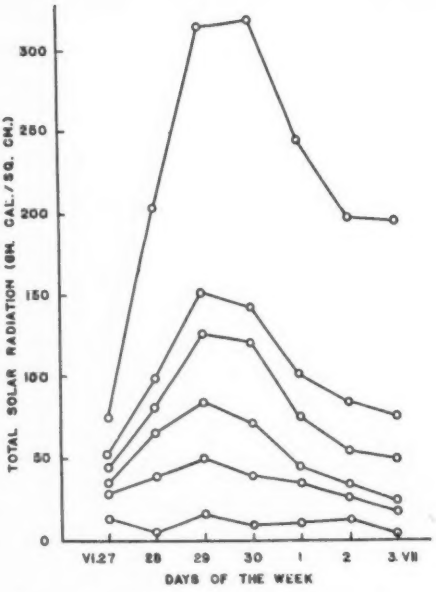

FIGURE 3. *Daily sums of total solar radiation in the open (upper line) and transmitted through various forest canopies.*

recently by Miller (1959), who states that "insolation from a plane, rather than a point source penetrates the canopy much more deeply. Insolation from all angles can find more points of entry into the stand than a single beam can, especially if the single beam comes in at a low angle." However, W. P. Lowry[4] insists that "even on a sunny day the sky radiation (reflected blue light) arrives at the earth's surface essentially from a 'plane' and at an absolute intensity exceeding that from a 'plane' of a cloud deck. The reduction in transmission is therefore only relative. And if beam radiation were substracted from the incident hemispheric total on a clear day, there would probably not even be a relative reduction."

The average daily radiation received in gram calories per square centimeter of surface of the receiver (after standard corrections) are given for the three study plots and for the open in Table 4.

Transmission of radiation in conifer stands is very low in general, and less than visual observation would suggest. Mean radiation over a period of 18 weeks was 2.4, 2.6 and 7.3 percent of that in the open, in mature thinned spruce stands of 688, 455 and 330 stems per acre respectively. In plot 3, a side effect, i.e., radiation transmitted under the canopy from the stand border, may be responsible for the initial high percentage transmission, and also in its rapid decrease. Other workers found values of the same magnitude for transmission through spruce crowns. Knuchel (1914), in his classical work on light transmission through the leaves and crowns of isolated trees and forest stands, indicates average transmission percentages of 13 for slightly thinned, mature stands of Norway spruce, and 4 to 5 in younger, dense stands. These values were instantaneous measurements with a spectrophotometer. Nägeli (1940) indicates 8 percent in spring and 4 percent in autumn in mature stands of Norway spruce. These figures apply however to the visible range only and do not take into account the infra-red radiation. Baumgartner (1952) observed in a young stand of Norway spruce the net all-wave radiation, that is, all the solar wavelengths both visible and infra-red, and the long, or thermal radiation from clouds and trees and ground. Miller (1959) arrived at an estimate of 5 percent solar-radiation transmission, by subtracting from Baumgartner's observations the flux of longwave radiation that probably was emitted by the foliage and by the ground. This estimate refers

TABLE 4. Total solar radiation per day during observation period.

Study plot	Total solar radiation	
	Percent	*gm cal/sq cm/av day*
In the open	100	168
1	2.39	4.01
2	2.58	4.33
3	7.31	12.28

[4]Personal communication.

consequently to the whole solar range.

Transmission percent seems finally to vary inversely with the number of trees per acre, at least in planted stands where trees are approximately uniform in size and regularly distributed (Tables 1 and 3).

Conclusion

It has been shown that transmission of total solar radiation is very low under high spruce canopies and that variations occur in a stand according to seasons and weather conditions. Both amounts and variations in solar radiation intensity in forest stands are important from the silvicultural point of view. The pyranometer used proved to be satisfactory and capable of detecting small differences in radiation intensity and is recommended for forestry purposes.

Summary

Total solar radiation was measured with spherical pyranometers throughout the day over a period of 18 weeks under three high closed canopies of Norway spruce plantations in the lowlands of Switzerland. Mean radiation under the three stands over the period was found to be 2.4, 2.6 and 7.3 percent of that in the open. Variations were dependent on stem density. The amount and variations of absolute and relative total solar radiation in gram calories per square centimeter both in the open and under the canopies are discussed. A short description of the spherical pyranometer is also given.

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The Structure and Increment of Beech Stands

Untersuchung über Aufbau und Zuwachs von Buchenbeständen. By Kurt Eiberle. Beiheft No. 31 zu den Zeitschriften des Schweizerischen Forstvereins. 83 pp. Zürich. 1960. (With English summary).

Review by R. Stahelin
Forest Service, U. S. Department of Agriculture

This publication discusses statistical tests of the influence of total volume, size of average tree, tree class, and stem quality on the value yield, based on plots established in 40, 60, 80, and 100-year-old beech stands in the Sihlwald near Zürich. Recommendations for further studies are proposed to provide an exact basis for the intuitive method of Schädelin's selective thinning. Individuals interested in growth and yield will find this publication instructive.

A Method for Calculating Error of Soil Moisture Volumes in Gravimetric Sampling

BY
JOHN D. HEWLETT
JAMES E. DOUGLASS

THE MOST commonly used means of measuring soil moisture has been the gravimetric method (Lull and Reinhart 1955). Expressed in percent by weight, these measurements are of limited value in determining quantities of water in the soil, and in many studies it is necesary to convert them to quantitative units, usually inches of water per unit depth of soil. Soil moisture expressed in percent by volume is a more convenient value, one which can easily be converted to inches, acre-feet, or pounds of water per cubic foot of soil. Most hydrologic studies, including those to determine evapotranspiration rates from soil moisture depletion trends, require moisture estimates in volumetric units. Such estimates are difficult to obtain by gravimetric methods.

The Gravimetric Method

The gravimetric method of soil moisture sampling, as used in this paper, refers to the process of determining volumes of soil moisture by separate sampling of bulk density and moisture in percent of ovendry weight of soil. Conversion of mean moisture by weight ($\overline{Pw}$) and mean density ($\overline{D}$) in grams per cubic centimeter to mean moisture in percent by volume ($\overline{Pv}$) for any plot or area is as follows:

$$\overline{Pv} = \overline{D}\,\overline{Pw} \qquad (1)$$

Separate measurement is generally made necessary because of the damage which would be done to the sampling site if the difficult task of extracting undisturbed samples were attempted each time moisture estimates are needed. Moisture samples are therefore extracted by use of King (Viehmeyer) tubes, augers, and other devices at each sampling date, and bulk density is collected only once.

Moisture sampling tubes now in use have sharp cutting bits .75 inch inside diameter, designed to collect about 85 cubic centimeters of soil per foot of depth. Because of compaction, it has been found impossible in most soils to calculate density from tube samples with any degree of accuracy. The most popular density samplers are roughly four times the diameter of the King tube and collect about 250 cubic centimeters of relatively undisturbed soil.

Usually, sampling has been carried out on plots of various sizes, depending on local terrain, but seldom larger than a few hundred feet square. Density and moisture samples are both located independently within the plot, or in some cases density samples collected in adjacent areas are assumed to be satisfactory for estimating mean density. The aim is to express the average amount of soil moisture for the entire plot, often by horizons or strata. Because of the great amount of time and work involved, seldom are more than one or two plots established in a soil-cover complex (population). For this reason, practically no information is available on variation from plot to plot within a type boundary, although some data on variation of moisture and density from point to point within plots have accumulated.

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The ultimate accuracy of an estimate of moisture in percent by volume is affected by many factors. For example, sample variation is associated with selection of plots in the field, since both microrelief and subsurface drainage on slopes affect the distribution of moisture in the profile. In some areas, rock content of the soil may be more important than all other sources of error in assessing soil moisture. Laboratory techniques and handling of samples contribute to error, not to mention many difficulties associated with instrumentation and field methods used to sample moisture and density. It may well be that optimum size of samplers has not yet been devised. However, it is not the intention to discuss errors related to mechanics of sampling. The chief concern here is with *precision*, which measures only the variation of the results obtained with the method, rather than *accuracy*, which depends upon detailed and accurate calibration of instruments (Taylor 1955). Most field and instrumental sources of error have been well reviewed by Lull and Reinhart (1955) and Olson and Hoover (1954), to whom the reader is referred for details of these difficulties and descriptions of various types of samplers employed.

There appears from the literature to have been little effort to treat the errors in gravimetric sampling, as defined above, in a systematic manner, although the method has been much used in agriculture, forestry, and hydrology. This paper is an effort to examine error introduced by separate sampling of moisture and bulk density, as well as possibilities for reducing such error. Theoretical developments are illustrated by means of data from two locations—the Coweeta Hydrologic Laboratory in western North Carolina and the Union Research Center near Union, South Carolina.

Determination of Error in the Gravimetric Method

The large number of samples required to provide adequate estimates of soil moisture in percent by weight, even on small plots, has been noted many times (Taylor 1955, Olson and Hoover 1954, Lull and Reinhart 1955). The size of plot is generally not felt to be as critical as the variation from point to point within plots. Lull and Reinhart first suggested that percent by volume values possess added error, because measurements of soil volume are involved. However, it has been generally overlooked that two variables are being sampled to yield moisture estimates in volumes, and that the standard error is compounded of their separate variances. Failure to account statistically for the error of the product, as in equation (1), makes it difficult to evaluate and compare many of the gravimetrically determined soil moisture volumes reported in the literature. It also tends to result in inefficient sampling designs, in which effort to increase precision by additional sampling may be applied to the variable contributing least to total error.

As generally carried out, estimates of loss from or addition to soil moisture are derived from successive measurements of total plot moisture. On the other hand, some studies call only for comparisons at one point in time between two plots under contrasting vegetation cover types. Without adequate replication of plots, the problem of precision in both types of study reduces essentially to determining error of independent estimates of plot moisture.

Density and moisture both vary from point to point within a soil horizon, but the variance of their product can be calculated if certain characteristics of the variation are known. Statistically, variance of the product of two mean variables is closely approximated by the following equation (Yates 1949):

$$S^2_{\overline{Pv}} = \overline{D}^2 S^2_{\overline{Pw}} + P_w^2 S^2_{\overline{D}} + 2\,\overline{D}\,\overline{P}_w\, r S_{\overline{D}} S_{\overline{Pw}} \qquad (2)$$

in which $S^2_{\overline{Pv}}$ = variance of mean Pv, an estimate of plot moisture content.

$S^2_{\overline{Pw}}$ = variance of mean Pw within the plot

$S^2_{\overline{D}}$ = variance of mean D within the plot

$rS_{\overline{D}}S_{\overline{Pw}}$ = Covariance of mean D and mean Pw

Equation (2) illustrates mathematically the consequences of being unable to sample Pv directly on undisturbed soil cores. It states that the variance of volume estimates is compounded of moisture, density, and their interaction. Some information about local means, variances, and covariance of moisture and density may be available for estimating the magnitude of expected sampling error. However, data on the variation of bulk density from place to place is scarce; seldom have sufficient numbers of density samples been collected to furnish reliable estimates of the standard deviation. Reported estimates of S_D vary from .05 to .20. Average variation of moisture (Pw) has been reported by only a few workers. Lull and Reinhart (1955) found standard deviation (S_{Pw}) to be about 4 percent, averaged from King tube samples at eight widely scattered sites. Taylor (1955), working with agricultural soils, reported a mean coefficient of variation of about 20 percent, or roughly 5 percent by weight. In sandy soils, S_{Pw} sometimes falls below 1 percent.

The third term in equation (2) concerns covariance of density and moisture. Reinhart (1954) has discussed correlation of D and Pw, pointing out that moisture content on a percent basis is generally dependent on density rather than density on moisture. His data indicated that when soils of variable density (but similar texture) are equilibrated under a given moisture tension in the "field capacity" range, moisture can be predicted from density with some confidence. Correlation coefficients (r) as high as $-.98$ were noted. The relation also held in the field when moisture contents were above the "dry" level.

It can be seen from equation (2) that if r is large and negative, considerable reduction in variance of Pv can be expected. Some method of sampling which allows determination of r must be devised if meaningful confidence limits are to be established for volume estimates of moisture. An effort was made in mountain forest soil to show that, if it is not feasible to measure

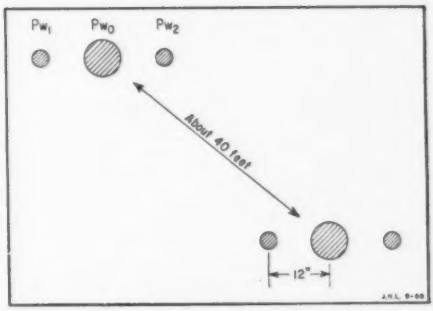

FIGURE 1. *Schematic drawing showing the arrangement of the clustered samples. Data summarized in Table 1.*

D and Pw on the same sample, the next best choice is to pair the samples as closely as possible.

For this purpose, a 10-acre hardwood area was selected at the Coweeta Hydrologic Laboratory of the Southeastern Forest Experiment Station. The soils are deeply weathered sand and sandy clay loams of granitic origin. The area selected bears a well-developed second growth stand of yellow-poplar, red maple, and hickory. Moisture and density values were determined on 60 undisturbed samples from the 2- to 8-inch soil strata, all secured at one sampling when the soil was not far below "field capacity." The 60 locations were distributed in a pattern such that each sample was about 40 feet from its nearest neighbor. Simultaneous sampling of moisture with a .75-inch diameter tube was carried out in the manner illustrated in Figure 1. These sample clusters were analyzed for density, moisture percentages, and correlation under field conditions.

Table 1 shows the values derived. Moisture in percent by volume (Pv) is shown calculated in several ways. Possibly the "best" estimate of total moisture in the 6-inch horizon is Pv_6, in which the actual moisture from undisturbed samples constitutes a direct measure of Pv. Other methods of calculation seem to result in higher estimates.

It should be observed that whenever

TABLE 1. Comparison of soil moisture estimates in percent by volume as calculated by various methods from the same data.

Bulk density and moisture estimates	Mean	Correl. with density	Standard deviation	Coef. of variation
Bulk density (250 cc sample)	1.082	—	0.15	.14
Pw_0 (from density sample)	35.16	—.87	6.1	.17
Pw_1 (tube sample 12" away)	35.40	—.76	6.2	.18
Pw_2 (duplicate tube sample)	35.64	—.76	6.2	.18
$\frac{Pw_1 + Pw_2}{2}$ (mean tube sample)	35.52	—.82	5.5	.15
Pv_1 ($D \times Pw_1$)	38.30	—	—	—
Pv_2 ($D \times Pw_0$) random pairing	37.85	—	8.7	.23
Pv_3 ($D \times Pw_0$) paired with neighbor	37.47	—	5.1	.14
Pv_4 ($D \times Pw_1$)	37.75	—	3.9	.10
Pv_5 ($D \times \frac{Pw_1 + Pw_2}{2}$)	37.66	—	3.5	.09
Pv_6 ($D \times Pw_0$) undisturbed sample	37.26	—	2.7	.07

mean D and mean Pw are multiplied, the resulting estimate (Pv_1 in the table) is higher than the mean of all products. The positive bias is the result of negative correlation of D and Pw. In this case, a bias of $+1.04$ Pv is introduced by this short-cut multiplication, which, because samples are not customarily paired, has been the usual method of calculation in soil studies. In addition to the bias, another limitation of this method is the lack of valid information about the variance of the product $\overline{D} \times \overline{Pw}$. Since it is impossible to calculate covariance where samples are collected independently, equation (2) does not apply. In this case, the only way to determine variance is through very costly replication of plots.

In calculating Pv_2, moisture and density values were paired using a table of random numbers and the standard deviation of the products derived. The actual products have a standard deviation of 8.7 percent (Table 1); calculated from separate variance by equation (2), the standard deviation is about the same. As expected, the correlation coefficient r is not significantly different from zero, so that the third term of equation (2) drops out.

Pv_3 is calculated by pairing moisture from each undisturbed sample with density of the neighboring cluster (40 feet away). Because r has some significance at this distance, the standard deviation (5.1), whether by equation (2) or directly from the products, is less than for Pv_2.

However, if moisture samples are collected with a King tube within a foot of the density sample, the correlation coefficient averages —.76 and Pv_4 is considerably less variable (standard deviation 3.9 percent). Variance estimated on this basis compares favorably with that estimated from the undisturbed samples (Pv_6).

One further comparison demonstrates the effect of increasing the number of moisture samples to two in each cluster, both collected within 12 inches of the undisturbed sample. Pv_5 is calculated by multiplying each density value by the mean of two adjacent King tube samples. The correlation is somewhat higher than when a single Pw sample is used. The standard deviation is slightly reduced, from 3.9 to 3.5 percent by volume.

It might be possible to solve precisely for the optimum combination of D and Pw samples per cluster if the correlation were known in advance. Since, however, correlation must be determined on the collected data, this is of limited value. Perhaps

the best rule of thumb is to base the proportion of density to moisture samples (within clusters) on the ratio of their respective coefficients of variation, estimated from prior knowledge of local soil conditions. From Table 1, the ratio would be .14/.18, or roughly one to one. One way to interpret this ratio is that just as much additional information would be secured by one more moisture as by one more density sample. In this case another moisture sample may be advisable, since the additional labor is small by comparison with that required to secure another density value. But it is also implied that a third moisture sample would supply very little information without additional density sampling.

Following the scheme outlined above, the total number of clusters, N, needed to sample an area of fairly uniform soil and cover conditions can be readily estimated from equation (2):

$$N = \frac{\overline{D}^2 S^2_{Pw} + \overline{P}^2_w S^2_D}{S^2_{\overline{P}v}} + \frac{2\,\overline{D}\,\overline{P}_w\, r\, S_D\, S_{Pw}}{S^2_{\overline{P}v}} \qquad (3)$$

Some prior knowledge of mean D and Pw, their respective variances and correlation, is needed to estimate in advance the clusters required to measure moisture in a soil strata to a given standard error. Generally the experimenter should have sufficient prior knowledge to gain a valuable lead on the size and nature of his sampling problem.

Application to Field Data

To demonstrate the use of this technique, comparison is made between soil moisture data at the Coweeta Hydrologic Laboratory and the Union Research Center of the Southeastern Forest Experiment Station. At Coweeta, soil texture is generally a fine sandy loam, and surface conditions have been relatively undisturbed in recent decades. Soils at Union Research Center contrast both texturally and in land-use history. Characteristic of the wide Piedmont belt of the Southeast, the soils at Union have truncated profiles. Under continuous cropping and subsequent abandonment, portions of the A and sometimes the B horizon have eroded away, leaving a 4- to 6-inch layer of sand at the surface.

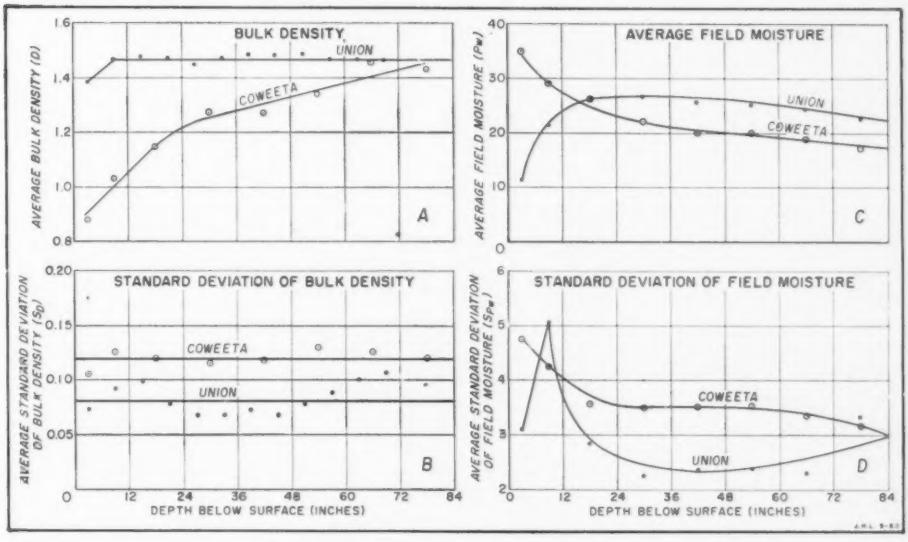

FIGURE 2. *A comparison of moisture and density variables which affect the precision of moisture estimates on plots at Coweeta and Union.*

The remainder of the profile is largely clay or clay loam.

The curves in Figure 2, compounded from thousands of observations in the two areas, illustrate differences between Coweeta and Union soils in moisture and density characteristics. Soils at Union are much heavier, but vary less than at Coweeta. However, there is a striking increase in bulk density with depth at Coweeta. The term "average field moisture" may be defined as the mean moisture (Pw) within specific strata around which seasonal or annual field moisture contents tend to vary. This follows from the fact that rainfall at the two centers is usually sufficiently well distributed to keep soil moisture fluctuating around a general level in each strata. Coweeta and Union (Figure 2c) illustrate trends in moisture content with depth below the surface.

Unfortunately, information about the correlation of D and Pw under various field conditions is scarce at both centers. Since the degree of correlation is crucial, the collected data must be relied on to furnish its estimate. But by using the average values from Figure 2 and assuming a range of correlation values, the size and difficulty of the sampling job necessary to meet study objectives can be estimated. Assuming, for the sake of illustration, correlation coefficients r equal $-.40$ and $-.80$, the number of clusters, each containing one D and one Pw sample, can be determined from equation (3). Table 2 contains these estimates for Coweeta and Union, giving N for a desired precision of one standard error equal 1 percent by volume (.12 inch per foot soil depth). Required numbers vary between strata; for example, the 6- to 12-inch layer at Union has proved to be particularly difficult to sample because of the textural discontinuity at the base of the plowed soil. Such layers might call for special treatment.

More important, however, Table 2 illustrates the influence of high correlation (assumed in this case) in reducing the size of the job in both types of soil. The data also illustrate the tendency for correlation to compensate for the seemingly erratic influence of separate variances in reducing sample numbers, particularly at Coweeta where density is light and variable. In the 6- to 12-inch layer at Union, however, an increase in correlation results in only slight reductions in N, possibly reflecting the mixture of two types of soil in this layer.

Discussion

Where normal variation in density does not involve drastic changes in texture, absolute volumes of soil moisture do not vary as much from point to point at Coweeta and Union as measurements on a percent-by-weight basis have indicated in the past. The standard deviation among 60 undisturbed

TABLE 2. The number of sample clusters (N) required at Coweeta and Union to hold expected standard error of moisture estimates to one percent by volume. (Data are listed for two assumed levels of correlation.)

Depth in inches	Coweeta		Union	
	$r = -.40$	$r = -.80$	$r = -.40$	$r = -.80$
0 - 6	22	7	16	13
6 - 12	18	6	47	37
12 - 24	17	7	15	8
24 - 36	17	8	11	5
36 - 48	18	9	11	5
48 - 60	19	10	11	5
60 - 72	19	11	12	6
72 - 84	18	10	15	8

samples of moisture volume referred to in Table 1 (Pv_6) was only 2.7 percent in quite variable forest soil. This constitutes a coefficient of variation of only .07, compared with .14 for density and .17 for Pw when measured separately.

Restricting gravimetric sampling to plots to reduce variation is therefore of little value unless many replications of the plot are possible, or the plot itself is the entire population to be sampled. In the former case, the optimum plot will most likely become the "cluster." In the latter case, paired samples within the plot will eliminate bias and help increase precision.

Consideration of the data in Table 1 and Figure 2 suggests that plot area limitation is not so critical as it may appear. Coefficients of variation in the 0-6 inch stratum, as determined from many 33 × 33-foot plots at Coweeta (plotted values in Figure 2) are .12 for density and .14 for moisture. Comparable coefficients on the 10-acre stand were .14 and .18, respectively. The increase in variance on the larger area is mostly compensated, in terms of moisture in percent by volume, by a corresponding higher correlation of D and Pw as their respective ranges increase. With a sampling design which takes advantage of correlation, the size of the sampling block may be less critical than is usually expected. Careful delineation of sampling areas to eliminate obvious differences in soil-vegetation cover types will usually be sufficient. Some additional precision may be obtained, as in any sampling problem, by arbitrary stratification into smaller blocks, each to be sampled by random methods. In this way the term "plot" becomes equivalent to "cluster" as defined above, and the collected data become more amenable to standard statistical treatment.

In general, moisture values which have an error greater than 1 percent by volume will be of little value in most comparative studies of soil moisture, whether comparison is from place to place, or from time to time. Using the tools referred to earlier, precision in the order of 1 percent will be hard to obtain where bulk density has a coefficient of variation .05 or greater. A 1-percent change in moisture in a 12-inch soil stratum is roughly the evapotranspiration to be expected on an average day. If it requires 10 to 20 sample clusters (Table 2) to provide this limited level of precision, the use of gravimetric sampling in studies of evapotranspiration at Coweeta and Union has doubtful possibilities.

Fortunately, newer methods are available. One now in fairly general use involves a radioactive source which emits "fast" neutrons. As these are slowed down by collision with hydrogen atoms (chiefly present as water in soils), their contact with a detector tube makes possible the measurement of the density of the moisture field surrounding the source. Thus, by neutron-scattering methods (Van Bavel 1958), soil moisture in percent by volume can be estimated independently of bulk density variations. Furthermore, by permanent installation of access tubes in field soils, changes in soil moisture with time can be observed directly in percent by volume, rather than as differences between two independent samples of moisture. When these instruments are perfected, their superiority in principle over the gravimetric methods may result in virtual replacement of the latter in many field studies.

Summary

The precision of estimates of soil moisture on a volume basis by gravimetric sampling methods is examined in theory, particularly as applied at the Coweeta Hydrologic Laboratory in the mountains of North Carolina and the Union Research Center in the Piedmont of South Carolina. The method most commonly used in research in hydrology, forestry, and agriculture is one involving separate measurement of bulk density and moisture in percent by weight, from which percent by volume contents are computed. It is shown that correlation between these two variables greatly affects the precision of estimate. A method of

calculating sampling error (instrumental error not separated) is presented, and its implications with regard to sampling design examined. Results indicate the importance of pairing density and moisture samples as closely together as possible, which leads to the conclusion that sample "clusters" are superior to plots, as the latter have been used. A field test is described in which the effects of different methods of calculating moisture in volumes are illustrated and compared.

Application of these techniques to average values of moisture, density, and their variances at the two research centers demonstrates the value of statistical methods in determining the size of the sampling job. It is pointed out, however, that even at best the limitations of the gravimetric method in these soils will for the most part preclude its use for hydrologic purposes.

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Responses of American Basswood Seedlings To Several Light Intensities

BY
WILLIAM CLARK ASHBY

SEEDLINGS of forest trees may be highly influenced by micro-environmental factors which are of little consequence to mature canopy trees of the same species. Shading, with all that the term may imply (Baker 1950, Holch 1931, Shirley 1945) is an important facet of plant competition both inter- and intraspecific. Successful seedling establishment and growth in American basswood (*Tilia americana* L.) has been observed by the author to be highly localized. When found at all, saplings and upper size classes of seedlings were observed most commonly in relatively open areas such as disturbed forests, edges of woods and adjacent fields, roadsides, or relatively open oak woods. Information on the relative growth vigor of basswood seedlings under shading, in the absence of root competition from other species, is necessary to interpret specific effects of light intensity on basswood's distribution and field localization.

The present studies were designed to provide such information for basswood seedlings in the Chicago environment. In them the relative growth of basswood at three degrees of shading was determined under garden conditions. Seed collections from several geographical areas were represented. Final determinations were made after 2 growing seasons. A supplementary study assessed basswood seedling growth at intensities of a few hundred foot candles under artificial light.

An evaluation of the adaptation of a given species to available habitats may often be made in terms of the age class structure for that species in the several habitats which it occupies. If basswood in the Chicago area were designated by the life form which had the greatest number of individuals within each age class, it would be considered an annual. Thousands of seedlings germinate and perish in areas which have few trees pole size and larger, and still fewer large seedlings and saplings. A slight increase in competitive advantage at the seedling stage could alter greatly the role of basswood in a stand.

The environmental conditions which had been important for the initial success of individual mature trees cannot be stated with any certainty. Within the life span of one large tree the microenvironmental factors may change greatly with development of the accompanying overstory and understory. The very great sprouting capacity of basswood results in many individuals within a stand representing more than one tree generation from the establishment of the original seedling, and compounds the difficulties of determining the nature of the environment at the time basswood became a component of the stand.

Materials and Methods

Three adjacent 4-foot by 8-foot plots on north-south axes were laid out in the Uni-

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The author, formerly Assistant Professor Department of Botany, University of Chicago, is now Associate Professor, Southern Illinois University, Carbondale. This investigation was aided by grants from the National Science Foundation and from the Wallace C. and Clara A. Abbott Memorial Fund of the University of Chicago. To Miss Ann B. Jacobson go thanks for her help in the taking and compilation of data. Manuscript received Aug. 27, 1960.

versity of Chicago Botany garden. Two of the plots had 4-foot high frames covered with shading material and open at the north end.

During the first season one frame was covered with a single and the other with a double thickness of cloth. Light intensities were measured from time to time with a quartz cell Weston light meter at mid-morning, noon, or afternoon. Intensities varied from one part of a plot to another, and at the several times of day. In these small plots the shading influence of the side walls and ends was relatively great. The light intensities in the plot with the single thickness of cloth diminished during the first season from about 30 percent of the full sunlight to below 15 percent as the cloth became dirty. Light under the double thickness diminished from about 12 percent of the full sunlight to below 5 percent during the season.

In the second season shade screening manufactured by Kaiser Aluminum was installed and left on throughout the following two years. Shade screening consists of a thin aluminum sheet punched out to form numerous small louvers. For the least shade the screening was mounted the opposite of its usual recommended orientation. The louvers thus opened toward the sun to let in filtered light. For heavier shade the screening was mounted in the usual orientation so that the louvers excluded direct light except in very early morning and late evening. Buildings or trees on the skyline gave much shade at these times. The light intensities in the two plots approximated 50 percent and 20 percent of noonday sun respectively. Although these intensities proved to be higher than expected or desired, further shading was not attempted. The unshaded plot, which lay to the west of the other two, was shaded briefly in the early morning by the frames on the shaded plots.

Temperature readings in the first year under the cloth shades were less extreme than those for the unshaded plot. Weekly maximums were depressed, occasionally by 10° F or more for the single cloth, and less so for the double thickness. This may relate to better ventilation under the single cloth. Minima, which were more nearly equal, tended to be a few degrees higher under the cloths.

During the second and third summers of the study minimum temperature readings under the aluminum shade screen again tended to be equal to, or slightly highly than, the readings for the unshaded plot. Maximum air temperature readings showed a less consistent relationship than under the cloths. They were frequently one or more degrees higher for the reversed shade screen than for the readings at the unshaded plot or for the plot with the shade screen applied in the conventional manner, which often had the lowest values. The maximum-minimum thermometer, Six's type, was mounted a few inches off the ground at the height of first year seedlings for the unshaded plot, and was suspended above the plants from the frame of the shade for the other two plots.

Seedlings at the several-leaf stage were transplanted to the plots in late spring or early summer. These plants had been collected in the field or raised from seed (Spaeth 1934.). Initial plant losses were replaced. There were 7 rows one foot apart, each consisting of 7 transplanted seedlings 6 inches apart, or of a variable number of seedlings which emerged from acid-treated and stratified seed planted in late spring. The plots received a light mulch of straw plus sheep manure or other fertilizers each season, and were watered during extended dry periods. The plants were infrequently sprayed or dusted with insecticides, chiefly to control red spider.

Data on origin is included in Tables 1, 2, and 3. The number and condition of leaves and branches and the condition of the growing point were recorded at intervals of 1 to 4 weeks depending on the growth stage of the transplanted seedlings. Derived values included: (1) time of bud break, (2) time of leaf loss, (3) number

of flushes of growth, (4) number of leaves per growth flush, and (5) number of leaves per week of growth. Heights were measured during the dormant periods or at harvest, which took place after approximately 2 growing seasons. By this time the seedlings were sufficiently large that crowding was becoming evident for some of the rows. Dry weights were determined for tops and gross observations were made on selected roots. The germination rows were each studied for one year in terms of germination and survival. Their dry weights were determined for the commercial Wisconsin accession. Two sugar maple (*Acer saccharum* Marsh.) seedlings were also included under each of the 3 shading conditions (Tables 1 and 2).

A second study was carried out in a temperature-controlled room with artificial light. Sixteen first-year seedlings collected from the Lake Michigan dune area of southwestern Michigan and planted in 3-inch pots were used per treatment. Differential light intensities were established by placing the seedlings at 2 distances from a light source consisting of two 40-watt fluorescent tubes. Two 60-watt incandescent lamps gave weak light from the side. During the first part of the experiment, at a temperature of approximately 66° F, light intensities for the two treatments were 500 ft-candles and 250 ft-c as determined by a Weston light meter with quartz cell. After 2 months the temperature was lowered to 62° F, and with the fall in temperature the light output decreased to be approximately 400 ft-c and 180 ft-c in the center of the seedling groupings. The light at the edges of the groupings was roughly 10 percent less. Data were taken on leaf number and stage of growth, and at harvest on dry weight and length. This experiment was started in July and terminated the following March. Nutrient solution was supplied at approximately 5-week intervals starting in September. Vigorous air circulation was maintained constantly past these plants.

Presentation and Interpretation of Results

Shading was shown to limit several aspects of basswood growth in a similar manner for all of the accessions studied (Tables 1 and 2). In a statistical comparison of all the transplanted seedling for the three shading treatments, a highly significant F-test for differences in dry weight was found (Table 1). This F-test was based on a partition of the degrees of freedom for shading and for accession. Both shading treatments differed at the 1 percent level from the unshaded treatment, and not from each other. No significant difference was found in the dry weights between the five accessions. The coefficient of variation was high, 120 percent. When evoluated on an individual accession basis, with consequent small numbers of degrees of freedom, F-values slightly exceeding the 5 percent level of significance were found for 2 out of the 5 accessions used. The fiducial limits overlapped slightly even for the no shade versus 80 percent shade. Coefficients of variations were over 100 percent except for one accession. This variability is shown in that dry weights of plants at 80 percent shade were in a few instances as great as that of those in full sun. The sugar maple values, with only 2 replicates, gave a low coefficient of variation of 12 percent. These seedlings grew significantly better in the heaviest shade compared to both half-shade and no shade.

Basswood plant height and leaf number in the second year showed the same relationships to shading within each accession as did dry weight (Table 2). The plants at 50 percent shade constituted an exception in that for one instance with each of the 2 criteria of evaluation they were larger than the plants in full sun. An analysis of variance computed for 1 (commercial unknown) of the 2 accessions which showed significant differences in dry weight likewise showed significance differences for stem length (5 percent level) and leaf number (1 percent level.) Statistical tests

TABLE 1. Top dry weight of transplanted seedlings after two growing seasons at three relative shading conditions.

Accession and origin	No. replicates	Dry weight (gms) 0% shade	50% shade	80% shade	Standard error g	F value	Statistical significance	Coefficient variation (percent)
			COMMERCIAL BASSWOOD					
1. Unknown	7	29.1	7.7	3.0	6.5	4.62	*	129
2. Central Wis.	7	11.0	5.4	3.8	2.8	1.83	n.s.	109
3. Central Wis.[1]	16-26	1.3	0.9	0.4	----	-------	----	-----
			NATIVE BASSWOOD					
4. Southern Wis.	7	28.2	5.9	4.1	6.0	5.05	*	124
5. Southern Wis.[2]	7	14.4	5.1	2.3	3.4	3.51	n.s.	123
6. Southern Mich.[2]	5	15.5	13.2	6.1	3.2	2.43	n.s.	61
			ALL BASSWOOD TRANSPLANTS					
1, 2, 4, 5, and 6. (see above)	33	19.9	7.1	3.7	2.1	15.74	**	120
			NATIVE SUGAR MAPLE					
7. Southern Wis.	2	0.5	0.7	1.2	0.1	29.0	*	12

[1]One season's growth of seedlings which emerged under the shading conditions.
[2]Single tree origin.
*Significant difference between the means at the 5% level; **Significant difference between the means at the 1% level; n.s. No significance demonstrated.

TABLE 2. Top growth of transplanted seedlings after two growing seasons at three relative shading levels.

Accession and origin	Stem length (cm) 0% shade	50% shade	80% shade	No. branches 0% shade	50% shade	80% shade	No. leaves (2nd season) 0% shade	50% shade	80% shade
				COMMERCIAL BASSWOOD					
Unknown	147	63	30	8.7	2.3	0.8	34	11	7
Central Wis.	70	38	23	2.3	2.0	0.2	26	15	10
Central Wis.[1]	13	11	8	0.3	0.1	0.0	12	8	6
				NATIVE BASSWOOD					
Southern Wis.	124	42	29	4.4	1.9	0.7	42	17	14
Southern Wis.[2]	79	35	26	2.1	0.4	1.1	26	10	12
Southern Mich.[2]	93	96	61	2.8	1.8	1.6	23	21	15
				NATIVE SUGAR MAPLE					
Southern Wis.	13	15	20	0.0	0.0	1.5	12	12	19

[1]One season's growth of seedlings which emerged under the shading conditions.
[2]Single-tree origin.

for values other than dry weight were not made on additional accessions. Well developed roots were present with 0 percent shade, and smaller roots under the shading conditions. Sprouting of those stumps not dug up was much more vigorous for the plants receiving no shade.

With 0 percent or 50 percent shade a ranking for height between the 5 accessions gave the same order of rank as for dry weight. The rankings for height at 80 percent shade and for leaf number at all degrees of shading were not in agreement with those for dry weight. It should also be noted that individual accessions varied in the proportionate dry weights at the 3 light intensities. For example, the 2 accessions from southern Wisconsin were

equal in weight at 50 percent shade, with one weighing twice as much as the other in the absence of shade.

A comparison of the data for activity of the growing points and of leaf condition for a given time period did not show great differences in response to shading. The greater number of leaves and length of stem in the absence of shading resulted chiefly from the cumulative influence of enhanced leaf production per growth flush, both terminal and lateral, and of a greater frequency of lateral bud break leading to leaf flushes and branch production. These differences were chiefly a result of extensive branching in the unshaded seedlings and of greater branching for those at 50 percent compared to 80 percent shade in all but one of the accessions (Table 2). Branch development was slight in the first growing season, averaging less than one branch per plant at the maximum, which was at 0 percent shade. Stem elongation in the second year accounted for 75 percent or more of the growth for the 2 growing seasons.

The number of leaves produced by a bud varied greatly within the seedling populations and was related to treatment. Under 0 percent shade continued leaf production for 15 weeks was recorded in several instances during the second growing season. The chief difference between the non-shaded and the shading conditions was the much greater number of actively growing shoots. No determinations were made of the number of leaves within a bud, which may vary with the growth vigor of the seedlings at the time buds are formed. Three to 4 was a frequent number of leaves for the first spring growth flush in all the treatments, and they were usually formed within 1 or 2 weeks, after which there was a gap of approximately one week before further leaf production commenced. Later in the season the number of leaves per equivalent duration growth flush was somewhat more variable, ranging from 2 to 5 and rarely from a minimum of 1 to a maximum of 6.

The maximum number of leaves produced in one sustained period (at least one leaf per two-week period) was 17 with 0 percent shade. Branch growth was as vigorous as that of the central shoot. For some plants, identification of the leader shoot was difficult, perhaps related to the partially sympodial type of growth in basswood. Under 50 percent and 80 percent shade the maximum number of leaves produced continuously on one shoot was 12. Less sustained leaf production was recorded for many of the branch shoots.

In the first growing season continuous leaf production reached a maximum of 6 leaves with 0 percent shade and decreased somewhat with the 50 percent and the 80 percent shade for 4 out of the 5 accessions. In the Michigan accession no effects of shading were evident. Branch shoots usually produced only 1 leaf at a time, though 3 leaves were recorded in one instance.

Growth vigor may also be represented as the average number of leaves produced per average number of weeks of growth. In the second growing season under 0 percent, 50 percent, and 80 percent shade respectively there were 7.38, 3.00, and 1.74 leaves produced per week of active shoot elongation for the commercial unknown accession; 2.05, 1.67, and 1.24 for the central Wisconsin (commercial); and 3.04, 1.74, and 1.35 leaves per week for the southern Wisconsin population. These values reflect strongly the branching characteristics of the seedlings. Fully comparable data were not available for the other 2 accessions.

The uppermost live buds started spring growth earliest. Bud break, which varied by only a few days between the 3 shading conditions, was slightly later under the condition of no shade, as was the time of cessation of leaf production. In the 1956 season leaf production terminated first with 80 percent shade, and in the 1957 season slightly earlier at 50 percent shade. Less detailed data for these determinations in the 1958 season showed earlier cessation of growth under 80 percent shade for the

Michigan accession and under 50 percent for the Wisconsin plants. The few sugar maple plants continued leaf production longest with 80 percent shade and ceased somewhat earlier at 50 percent than at 0 percent shade. The time of the first shedding of leaves by basswood was not consistently related to the shading conditions. Completion of leaf fall was latest with no shade and usually earliest under 80 percent shade, the differences occasionally amounting to as much as 5 weeks. Unpublished studies by the author have shown that chilling greatly stimulated bud break for leafless plants. The presence of first-year branches and of successive growth flushes on one axis establishes that dormancy is not an inherent characteristic of this temperate zone species simply consequent upon bud formation.

Emergence, survival, and growth responses to shading for the plants of 4 geographical accessions (Table 3) started directly from seed were quite irregular. Emergence, which ranged from 23 to 64 percent, was for all accessions greatest in one of the shading conditions. Time of emergence was delayed slightly with shade, however. Survival ranged from 54 to 100 percent of the germinated seedlings and again was always greatest in one of the shade conditions. The seedlings of the central Wisconsin (commercial) accession (Tables 1 and 2) were progressively limited in dry weight with increased shading.

Further influences of shading on the environment of these seedlings were evident. Under the 80 percent shade in the garden the soil remained obviously moist for extended periods after a rain compared to the other plots. It also remained frozen several weeks longer in the early spring than the others. Moss growth was evident on the soil surface in this plot. The unshaded plot was most unlike the 80 percent shade in these respects. Moss growth was particularly evident on the soil surface of the plants grown under the controlled temperature and light conditions. At 400 ft-c were present mats consisting of *Bryum argenteum*, *Leptobryum* sp. and *Physcomitrium turbinatum*, and also of *Marchantia polymorpha* and *Oscillatoria sancta*. *Bryum argenteum* and some fern prothallia were identified from a lesser growth at 180 ft-c. Paul D. Voth of the Department of Botany, University of Chicago kindly furnished these identifications.

The experiment using artificial light at controlled temperatures showed poor growth for the Michigan seedlings. Leaf initiation and development ceased almost as soon as the plants were placed under the test conditions. As this study was carried out before it was known how sensitive basswood may be to nutritional conditions (Ashby 1959), the supplemental fertilization may have been inadequate. Nine of the 16 plants at 400 ft-c still retained leaves at harvest, compared to 4 of the 16 plants at 180 ft-c. Nearly half of the plants retained the true terminal bud, a characteristic of this Michigan material in several other studies, which is at variance with the

TABLE 3. Percentage emergence and survival of basswood at three relative shading levels.

Accession and origin	No. seeds in sample	Percentage emergence			Percentage survival		
		0%	50%	80%	0%	50%	80%
Commercial							
Central Wis.	50	44	52	32	54	100	81
Native							
Northern Ill.	50	56	54	64	72	93	100
Northern Ind.[1]	100	46	55	35	87	96	86
Southern Ohio[1]	100	23	24	45	87	83	93

[1]Single tree origin.

usual sympodial growth in basswood.

Total final dry weights were 0.98 gm at 400 ft-c and 0.30 gm at 180 ft-c. Because of the greater number of leaves remaining at the 400 ft-c, the two treatments were statistically analysed in terms either of stem weight or of stem plus root weight. For both comparisons the analysis of variance demonstrated highly significant differences between the treatments. The coefficients of variation were 67 and 73 percent for these two tests, showing less variability for these pot-grown plants under controlled conditions than in the garden. The top (stem only)-to-root ratios were 0.23 and 0.37 for the 400 ft-c and the 180 ft-c, a consequence of the proportionately greater limitation of root growth at the lowest light intensity. The values for top-to-root incorporating the remaining leaves were 0.30 and 0.40. Roots were observed at harvest to be growing on 4/16, and 6/16, of the plants in the two treatments. Two plants in each treatment had obvious mycorrhizal roots. Presumably all of these field-collected seedlings would have been exposed to mycorrhizal infection.

Discussion

Basswood has been reported to be tolerant of shading (Baker 1950). Cribbs (1919) stated that trees when growing in open situations had more vigorous growth which remained active later in the summer than in the forest. Holch (1931) compared the growth of basswood, walnut, hickory, red oak, and bur oak seedlings for 3 years on 2 forest, and one open, "prairie," site. Shading aided initial survival. Subsequent growth of the survivors was much greater in full sun than at either an oak station where maximum light intensities reached 21 percent, or a basswood station where maximum light reached 10 percent, of full sun. The poor growth of basswood under shade is illustrated by the leaf numbers. At the end of three years they were 2, 3, and 18 for the basswood, oak, and "prairie" habitats. Basswood, which made poor growth relative to the other species was, however, the only species alive after 2 (and 3) years at the basswood station. Size of tops and roots after 3 years at the 2 forest sites were essentially the same as for the first year seedlings. At the prairie site they had increased greatly by the third year.

An individual seedling's vigor seems to be highly related to the extent to which its buds keep growing. With the delayed germination characteristic of basswood and a fairly frequent incidence of seed years, first-year seedlings whose photosynthetic surface consists of cotyledons as well as of 1 to 3 leaves, even under appreciable shade, may be able to occupy an opening as quickly as highly suppressed survivors from an earlier year. Under improved growth conditions the number of branches, number of leaves resulting in still further axillary buds, the foliage area, and physical occupancy of a site are all increased. These in turn presumably lead to increased total photosynthesis, dry weight production, and size of root system, all of which make for a vigorous seedling and enhanced survival. The ability of basswood to occupy a given habitat may rest essentially on such an ability to keep growing. Further factors of the environment, such as nutrients (Ashby 1959) and soil temperature (Ashby 1960) must likewise be suitable for the growth of this species. The present studies emphasize the limitation to shoot growth from shading. They further showed the importance of the cumulative effort of perhaps not very great differences in any one response to light intensity such as lateral bud break, number of leaves per growth flush, and length of retention of leaves. This effect was found by Holch (1931) in that the first year results were much less divergent for the three stations. The high amount of variability shown for basswood seedlings in response to shading relates to interpretations from field studies. A response observed for one seedling may not at all be typical of the population as a whole and may therefore be of much less significance.

Two facets of the present findings: that height is not a good criterion of dry weight production at low light intensities, and that seedlings under adverse levels of an environmental factor may suffer greater mortality in their weakened state, have been proposed by earlier workers (Baker 1950, Shirley 1945). For example, the greater top-to-root ratio at 180 ft-c as contrasted to 400 ft-c would increase the probability of seedling mortality from drought, particularly in competition with other species. Effects of competition on basswood are suggested in that even at the 80 percent shade in the present study growth was much better than that reported by Holch (1931) in an oak stand with relatively equivalent average light intensity. The conclusions to be drawn are that basswood is limited in its growth by the shade of any except the most open forest stands and that vigorous basswood is unlikely to be found under forest canopies. The higher soil temperatures of forest openings likewise are suitable for greatest growth of seedlings (Ashby 1960). Basswood reproduction from seed may be related to a gap phase in the history of a vegetation stand such as outlined by Watt (1947). This conclusion is in agreement with reports of basswood regeneration (Scholz 1958, Stearns 1951). Sugar maple, on the other hand, showed enhanced growth with shading which is in keeping with its reported reproductive characteristics under forests.

Summary

1. Dry weight of transplanted basswood seedling populations after 2 growing seasons was highly significantly less with 50 percent or 80 percent shade than with full sun. The coefficient of variation was 120 percent. Statistical tests based on individual accessions showed significant differences in growth under shading for only 2 of the 5 accessions.
2. Stem length, number of leaves, and number of branches were limited by shade.
3. The greater growth of unshaded plants was related to a cumulative differential vigor which can be expressed in terms of number of lateral shoots, number of leaves per growth flush, number of leaves per week, and delay in leaf abscission.
4. In several instances enhanced germination and first-season survival were found with shading. The surviving plants made less growth than those in full sun.
5. The progressive reduction in seedling size with decreased light intensity was demonstrated with artificial light of 400 compared to 180 ft-c.
6. Sugar maple grew progressively better with increased shading.

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Dynamics of Even-Aged Forest Stands

By M. S. Czarnowski. Louisiana State University Press, Baton Rouge 3, Louisiana, 132 pp, illus, May 15, 1961. $5.

Review by Austin A. Hasel
Forest Service, U.S. Department of Agriculture.

Interesting and stimulating throughout, this compact book presents a new and comprehensive theory on the development of pure, even-aged forest stands. The objective is to unravel by quantitative methods the relationships among parameters that characterize pure, even-aged stands—age, average diameter, average height, number of trees and volume per acre—and thereby reduce long, cumbersome tabulations to a few essential formulas.

The theory includes two major hypotheses:

(1) $N = N' \quad \frac{43{,}560}{H^2}$

and

(2) $d = a(H\text{-}4.5) \quad \frac{2}{Z+1}$

wherein

N = number of trees per acre in a normal stand

H = mean height of stand (or of the dominant trees) in feet

N' = number of trees on $(H)^2$ square feet of surface in a normal stand

= site indicator (constant value for a site class and independent of age)

d = average stand diameter breast high

a = coefficient of proportionality (depending on stand "compactness")

Z = crowding factor (stocking)

$= \frac{\textit{actual number of trees per surface unit}}{\text{normal number of trees per surface unit}}$

$= \frac{Nr}{N}$

On the basis of comparisons of deductions from these hypotheses with relationships developed by other investigators, the author concludes that the latter are particular cases of formulas (1) and (2). Comparisons are made with Köhler's Generalization (area occupied by a tree in normal stands of Scotch pine is equal to the square of 1/6 of the tree's height, regardless of age), Khil'mi's Theory, Chisman and Schumacker's Tree-Area Ratio, Bistrup's Formula, and others. It is likely that the new measure of stand density reported by Krajicek *et al.* (FOREST SCIENCE 7:35-42) was not available in time for inclusion in these comparisons.

One chapter is devoted to application of the hypotheses to the problem of determination of the maximum attainable volume per acre. Another chapter treats of the use of crown-length ratio as an index of degree of crowding (stocking). A chapter on application of the theory of forest practice outlines solutions to the problems of choice of proper degree of thinning, calculation of allowable cut, and determination of the optimum level of growing stock in connection with use of the Austrian formula.

The author makes no claim that all problems concerning the dynamics of pure, even-aged stands are solved in this volume. Stands in which the trees are irregularly distributed area-wise are not considered, for example. Such stands are common in the U.S.A. The problem of evaluating stocking and stand condition in clumpy stands involves additional parameters to express degree of occupancy of area by trees, and how much of the stocked area is in fact over-stocked.

The author's intention of arousing "the reader's interest in this subject which is of considerable importance to future forest research and practice" will unquestionably be realized. The theory presented warrants careful testing with experimental data for various types and sites in addition to the numerous tests presented.

A Computer Technique for the Study Of Forest Sampling Methods

I. Point Sampling Compared with Line Sampling

BY
MARSHALL N. PALLEY
W. G. O'REGAN

THIS PAPER describes the development and some applications of a procedure for the empirical study of forest sampling methods with the aid of an electronic computer. The procedure was developed with particular reference to Bitterlich's (1948) point sampling and Strand's (1957) line sampling methods. It has been applied to forest stands in three different California forest regions. The procedure has afforded a useful comparison of some of the characteristics of the two sampling methods, and it may be useful in evaluating other methods of forest sampling.

The study of forest sampling methods helps to interpret the results of sampling which has already been done. It may enable us, for example, to make probability statements about the interval within which a certain forest parameter is contained. In addition, understanding of sampling methods helps in making recommendations about how to sample in particular cases. We may be able to offer some guidance on the size, constitution, and number of sampling units needed to gather particular information about given forest stands.

It is possible to study forest sampling methods by making inferences from the results of actual sampling trials. An alternative is to identify and study all the elements of the population from which samples may be composed. This latter approach underlies the conception of forest sampling we propose. The computing technique developed here is founded on this conception of sampling and makes possible its numerical realization.

In this paper, we identify first the population of interest in forest sampling in general, and in point sampling and line sampling in particular. The roles of elementary sampling units, of probabilities of selection and of measurement characteristics, are discussed and distinguished. We then pass from a simple example of listing the entire population in random point sampling to a computer program which approximates the conceptual populations defined by point and line sampling in forests containing a larger number of trees. Finally, the results of applying this technique to actual forest stands are presented and the significance of these results in adding to knowledge of the characteristics of these sampling methods is discussed.

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Theory

The conceptual population in forest sampling. As a preliminary step in working with forest sampling methods we put forward a generalization which we find helpful: a forest sampling method generates a conceptual population when considered in relation to a specific forest. It takes two components to bring this conceptual population into being. It takes the physical population of trees growing on a particular piece of forest land. And it also requires that these trees be partitioned into elementary units according to a sampling rule. The conceptual population is the aggregate of all these elementary units. Different sampling rules applied to the same forest define different conceptual populations. Similarly, the same sampling rule applied to different forests defines distinct conceptual populations.

The elementary unit in forest sampling is typically a group of trees. For a given forest, the constitution of these groups of trees depends upon the sampling rule used. An example of one rule for sampling is the following: divide a forest into N mutually exclusive plots of equal area, a, and draw these plots and the groups of trees which they contain at random. Then the number of elements in the conceptual population defined by this rule and a forest of size L would be $N=L/a$.

Understanding of the conceptual population involves several aspects that go beyond the physical delimitation of the elementary sampling units. One such aspect relates to the probabilities that each of the elementary units will be drawn when sampling is done in a prescribed way. In a random drawing from the N plots in the forest the probability that any one unit will be drawn is the same for all units, namely $1/N$. Finally, the conceptual population becomes meaningful only in terms of one or more measurable characteristics whose numerical value can be determined for each of the elementary units. In our example these characteristics might be number of trees or total volume. The characteristic "number of trees" would then be defined as the number of trees on the plot divided by the ratio of plot area to forest area.

To make progress in the understanding of forest sampling methods, it is necessary to work with the conceptual population. We may deal with this population by mathematical analysis or, alternatively, we may approach this population empirically, in terms of specific numerical examples. Sampling rules lend themselves readily to mathematical formation. More difficulty is encountered in finding meaningful mathematical expressions which generalize the complex ecological relationships of forest trees. For lack of adequate theory on the locational patterns of trees, we must undertake the empirical study of these conceptual populations.

To give focus to our endeavor, we limit our attention to the point sampling and line sampling methods of sampling. In an earlier paper point sampling and some of its variant forms were considered analytically (Palley and Horwitz 1961). The unbiasedness of these methods was explored and expressions were derived for the true variances of the estimators appropriate to these methods. It was clear from this work that the variance of the estimators depended on the amount and distribution of basal area in the forest, on the size of the sampling angle, and on the number of points making up a sample. An important term in the formula for the variance depended on the size of the trees and their unspecified plan positions in the forest. The present treatment of the subject differs from that of the earlier paper in two respects. First, it is oriented toward specific forest stands of known characteristics rather than toward a general forest in which the sizes and positions of the trees are unknown. It is in this sense that the approach taken here is empirical.[1] Secondly, we are concerned with the elements of the conceptual population, whereas formerly samples of n elements out of the conceptual population

[1]The analytical approach is pursued further by Hirata (1958) by making assumptions about the spatial distribution of trees.

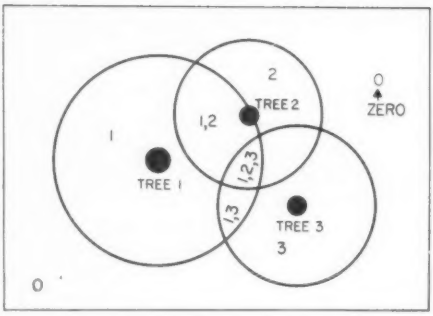

FIGURE 1. *Clusters of trees and regions in the conceptual population defined by point sampling in a forest of three trees.*

were dealt with as the fundamental building blocks.

Point- and line-sampling populations. The nature of the conceptual population in random point sampling may be illustrated in terms of the simple forest pictured in Figure 1. The shaded spots represent the three trees contained in this forest. We recall that to construct a sampling unit a point is taken at random within the land area of a forest. Any trees in the forest which are nearer the sampling point than a constant multiplier times the tree radius are included in the cluster of trees associated with that point. The locus of points which will have tree 1 associated with them is the circle which has for center the center of tree 1 and for radius the chosen constant, K, times the radius of tree 1 (Grosenbaugh 1958). This is the large circle surrounding the first tree in Figure 1. Similarly K-circles for trees 2 and 3 of Figure 1 have for their radii the lines which are K times the size of their respective tree radii. In the forest pictured in Figure 1 the rings surrounding trees 1 and 2 overlap. By the rule for inclusion of trees, all points within that area of overlap will have both trees 1 and 2 associated with them. We will denote as a *cluster* those trees associated with a point by the point-sampling rule. Thus, a point in the mutual overlap of trees 1, 2 and 3 will have all three trees included in its cluster. Also, in this forest, any point drawn outside the area of the tree rings will have no trees associated with it. We may make the following generalizations regarding point sampling:

1. The number of trees in a cluster may be any number from 0 to N, where N is the total number of trees in the forest.

2. The same cluster of trees may be associated with more than one point.

3. A particular tree may be included in more than one cluster.

4. The number of clusters possible in a forest is finite.[2]

These distinctive clusters of trees which are identified when the point sampling rule is applied in a particular forest are the elementary units in random point sampling. All of the elementary units in the forest pictured in Figure 1 are listed in the first column of Table 1. Although the number of possible sampling points is infinite, these sampling points are grouped in regions such that all the points within a given region refer to the same cluster of trees. A region may accordingly be defined as the set of all sampling points which have a common cluster of associated trees. Each of the discrete areas pictured in Figure 1 is the geometric representation of a region. The designation of the region indicates the trees in the cluster associated with that region.

The concept of the region leads directly to the statement of the probabilities that each of the elementary sampling units will be drawn. The land area of the forest of Figure 1 is the fundamental probability set, and the regions bounded by the intersection of the tree rings and the edge of the forest are the elements of this set. If we denote the area of the ith region as R_i and the land area as L, then the probability that the ith cluster of trees will be drawn is the ratio of the area of its corresponding region

[2]The bounds on the number of clusters, M, would be $1 \leq M \leq \sum_{j=0}^{N} C(N,j)$. The upper limit would in practice be much lower than the sum of combinations indicated in a forest of even moderate extent.

TABLE 1. List of elementary units, total volume measurements, and probabilities of the conceptual population created from a forest of three trees by the choice of K *and the point sampling rule.*

Trees in cluster	$\frac{K^2}{L}$ · total volume[1]	Probability of selection[2]
0	0	$\frac{R_0}{L}$
1	$\frac{z_1}{b_1}$	$\frac{R_1}{L}$
2	$\frac{z_2}{b_2}$	$\frac{R_2}{L}$
3	$\frac{z_3}{b_3}$	$\frac{R_3}{L}$
1, 2	$\frac{z_1}{b_1} + \frac{z_2}{b_2}$	$\frac{R_{1,2}}{L}$
1, 3	$\frac{z_1}{b_1} + \frac{z_3}{b_3}$	$\frac{R_{1,3}}{L}$
2, 3	$\frac{z_2}{b_2} + \frac{z_3}{b_3}$	$\frac{R_{2,3}}{L}$
1, 2, 3	$\frac{z_1}{b_1} + \frac{z_2}{b_2} + \frac{z_3}{b_3}$	$\frac{R_{1,2,3}}{L}$

[1] z_i = volume of ith tree ($i = 1, 2, 3$).
b_i = basal area of ith tree.
[2] R_j = area of the jth region.
L = land area of the forest.

to the land area, R_j/L. These probabilities of selection are given in the third column of Table 1.

The final stage in the listing of the population is to select a characteristic of the population which can be evaluated numerically. For purposes of illustration we select the characteristic total volume, defined as being proportional to the sum of the ratios of volume to basal area of the trees making up the cluster. The constant of proportionality is L/K^2, where L is the land area of the forest and K is the ring multiplier.[3] The values of this characteristic for each cluster of trees are given in the second column of Table 1. From this completed population list, we can calculate if we wish population parameters such as the expected value and variance of total volume.

We are now in a position to distinguish three populations which play a part in point sampling. The population of points is used to identify a cluster of trees. The population of clusters of trees (with associated measurement characteristics) is the population from which samples are drawn. This conceptual population has some parameters (expected values of measurement characteristics) which correspond to similar parameters for the basic population of individual trees in the forest. The conceptual population has other parameters, for example, variances, which have no directly corresponding representation in the forest itself. Of course, the forest sampler is chiefly interested in the ultimate population of trees. But he must also keep in view the conceptual population in order to assess the reliability of the inferences he may make about the forest from his sampling.

When we turn to line sampling, a parallel development of the elements of the population, measurement characteristics, and probabilities may be made. According to the line sampling rule, all of the trees whose perpendicular distance from a line is less than K times their diameters are included in the cluster of trees associated with that line. These K-diameters are illustrated in Figure 2 for a forest of three trees. For simplicity we work with lines which extend the full length of the forest. Two or more trees may be associated with a line only if the line intersects their K-diameters. The rectangles of Figure 2 are the regions corresponding to the distinctive clusters of trees arising from line-sampling

[3] It is shown elsewhere that this definition leads to an unbiased estimate of total volume in the forest. (Palley and Horwitz 1961).

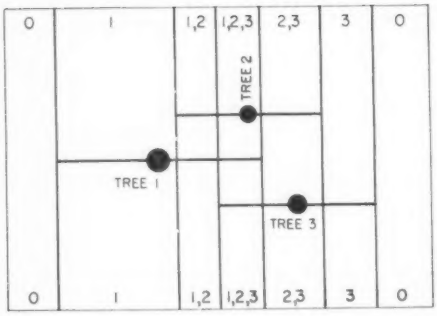

FIGURE 2. *Clusters of trees and regions in the conceptual population defined by line sampling in a forest of three trees.*

with a given value of K and a fixed sampling direction. The probability that any cluster will occur in such random line sampling is determined by the ratio of the area of its region to the area of the forest.

The measurement characteristics in line sampling are made up of the contributions of the trees making up the cluster. Since these trees are chosen with probability proportional to their diameters, each tree characteristic is divided by tree diameter before being added to the measurement characteristic for that line. The line sampling characteristic for total volume, for example, turns out to be $L/K \sum_{i=1}^{m} \frac{z_i}{d_i}$ where z_i and d_i are volume and diameter of the ith tree in a cluster of m trees.

Computer Simulation

This method of listing the entire population could be generalized as a graphical technique serviceable in forests containing a large number of trees. A few attempts to do this, however, will suggest how lengthy and how subject to error such an undertaking would be. To shorten the process and minimize the chance of making mistakes, we adapt this procedure to the capabilities of a computer.

The computer method is founded on approximating the population list by the use of a closely spaced line and point grid. This grid serves both to identify the elements of the conceptual population and to approximate the areas of the regions corresponding to each of these elements. The required areas are approximated by the principle of the dot grid or line intercept: the area of an irregularly shaped surface is proportional to the number of dots (or number of line intercepts) contained in relation to the total number of dots (or number of lines) in the entire forest area.

For the basic grid of lines and points we define a rectangular co-ordinate system over a square forest of 2.5 acres, 100 units to a side. The lines of this system which parallel the y-axis are taken as the lines of the line grid. The intersections of these lines with those which run in the x-direction are taken as the points of the system. The co-ordinate system thus defines a system of 100 lines each five chains (330 feet) long extending across the entire forest, and 10,000 equally spaced points 5 links (3.3 feet) apart. The basic forest size of 2.5 acres is chosen in relation to the availability of stem maps of measured forests and the memory capacity of the IBM 701 computer. Forests of other sizes may be introduced, up to a maximum of 220 trees.

For measurement characteristics under both point sampling and line sampling we choose number of trees, total basal area, and total volume. The data to be supplied to the computer consists of the co-ordinates, the diameter, and the cubic volume of each tree in the forest. For successive trials the value of K, the cosecant of half the sampling angle, can be made variable.

The computations are performed in three phases: (a) calculating and storing the measurement characteristics for each tree in terms of both point and line sampling: (b) associating the trees with each of the 10,000 points and 100 lines in the forest, and accumulating the corresponding point and line measures; (c) finally, computing for each of the statistical populations so defined the variances, covariances, correlation coefficients and co-efficients of variation. For convenience we may refer to the

results of these three steps as the tree table, the point and line table, and the table of population parameters. Convenience in programming and testing the work led to the use of three consecutive computer programs. The first program takes the tree data and produces the tree table and the point and line table, the latter written on magnetic tape. This tape serves as the input for the second program in which the population parameters for point sampling are printed and the line measures are punched out on binary cards. These binary cards are used in the third program to compute and print the parameters associated with the line sampling method.

The process needed to fill out the tree table may be explained by considering the total volume characteristic of a tree in a hypothetical forest. Suppose that a certain tree in the forest has a volume of 300 cubic feet and a diameter of one unit. Then if the value of $K=20$, the ring radius of this tree is 10 units, and the area of the K-circle is 100π square units. As we saw in connection with Table 1, the tree contribution, c, for total volume, would be:

$$c = \frac{L}{K^2} \cdot \frac{300}{\pi/4 \cdot 1^2}$$

$$= \frac{10{,}000}{400} \cdot \frac{1200}{\pi} = \frac{30{,}000}{\pi}$$

the land area being equal to 10,000 square units. Now if the K-circle of this tree overlaps the edge of the forest such that just two-thirds of the K-circle is within the forest, then the tree contribution, c', must be adjusted. We then would write:

$$c' = \frac{30{,}000}{\pi} \div \frac{2}{3}$$

$$= \frac{45{,}000}{\pi}$$

To find the proportion of the K-circle of edge trees which is within the forest, the computer makes a point count to approximate this area and compares it with the computed area of the full K-circle. A similar adjustment must be made for edge trees in relation to line sampling. The completed tree table contains six entries for each tree in the forest, three point sampling characteristics and three line sampling characteristics.

In the second phase of the computer process, the clusters are identified in relation to the 100 lines and the 10,000 points. We take the first line and ask, "Does the first line intersect the K-circle of the first tree?" If it does, we add the line-sampling measures for the first line. Now we ask, "Does the first point on the first line fall within the K-circle of the first tree?" If the answer is yes, we add the point sampling measures of the first tree to appropriate sum registers for the first point. We continue with points on the first line until we reach one which does not fall within the K-circle of the first tree. Now we are ready for the second tree in relation to the first line and the points of the first line. All of the trees are tested in relation to the first line. The results for the first line and the first 100 points are now written on magnetic tape, and the memory is cleared for the accumulation of the second line and the second 100 points. The process goes on until the 100th tape record is written, the completed point and line tape requiring 10 or 15 minutes of computing time, depending on the values of K and of N. In effect, we have tested for the inclusion of every tree at every point and at every line and added in its measurements as required.

The completed tape contains a list of 10,000 points and 100 lines and their associated measurement characteristics. Those points (or lines) associated with a common cluster of trees have identical measurement characteristics. A frequency table could be constructed by combining points and lines representing the same cluster of trees, thereby approximating the probabilities of selection of each cluster. It is more efficient of computer time to omit this step and work directly with the unordered list. Under control of a second computer program we call in the tape and compute the means, variances, covariances, and correlation coefficients of the array of measurements of number of trees, total basal

area, and total volume. The third program performs equivalent computations for the 100 groups of line sampling characteristics.

The parameters of populations of 10,000 points and 100 lines are approximations of the parameters of the conceptual populations based on clusters of trees. To test the closeness of the approximation, we evaluate the means and variances of a simple forest numerically and compare them with the results given by the computer. The true variances of the conceptual populations are calculated by formula (Palley and Horwitz 1961). The results of these comparisons are given in Table 2. The approximations are all within two percent of the true population parameters. We note that the computer results form part of a distribution of approximations which might be generated by moving the starting point of the grid by small increments through the 3.3 foot interval.

Results

Trials in representative forests. This technique can now be applied to some plot data and stem maps taken from actual forests. We may hope in the process to gain some insight into the characteristics of point and line samples applied to forests which differ in the number, size, and arrangement of their trees. Further, we may examine the effect of changing the sampling angle (the value of K) on the variability of the resulting populations.

The first example is taken from Compartments F and L of the University of California Special Use Forty on Little Schneider Creek.[4] The forest is an old-growth stand of mixed conifers on the west side of the Sierra Nevada at an elevation of 3,500 feet in Plumas County, California. We select two 2.5 acre compartments which lie on the same ridge. These are typical high-site stands on deep soils with trees up to 6 feet in diameter and 200 feet in height. The stocking of trees over 13 inches in diameter is not more than 50 stems per acre (Table 3). The volumes of the two compartments are nearly equal, but Compartment L contains more trees.

The simulation and computing procedure is now applied to the two stands for each of five values of K, namely 20, 25, 35, 40, and 50. These values of K correspond to a range in prism diopters of 4 to 10, and of basal area factors on a per acre basis of approximately 15 to 100 square feet of basal area per tree selected.

Certain important trends and regularities emerge from the results of these trials (Table 4). There appears to be a small systematic difference between the total basal area in the forest and the total basal area for the various defined populations. This difference diminishes as K increases. We regard this error as unimportant and attribute it to the failure of a point count to measure exactly the areas of circles. The defined population totals for number of trees and cubic volume agree to four significant figures with the forest totals. Within the range of values of K used we observe

TABLE 2. Comparison of the parameters of a conceptual population based on a forest of six trees and a chosen point sampling rule with those of an approximation based on the same forest, the same angle gauge, and a grid of 10,000 points.

Parameter	Magnitudes	
	Conceptual population	Based on 10,000 points
Number of trees	6.00[1]	6.00
Total basal area	3.36[1]	3.34
Total volume	1,729.00[1]	1,728.00
Variance of number of trees	355.07	347.00
Variance of total basal area	55.37	54.67
Variance of total volume (thousands)	15,057.00	15,148.00

[1]These are also parameters of the forest.

[4]Measurements and maps kindly supplied by courtesy of Professor F. S. Baker. Volumes determined by local volume table.

TABLE 3. Characteristics of the four forests used to illustrate the computer technique.

Name of forest	Ave. d.b.h. (inches)	Diam. range (inches)	No. of trees per acre	Basal area per acre (sq. ft.)	Volume per acre (cu. ft.)	No. of trees	Total Basal area (sq. units)[1]	Total Volume (cu. ft.)
Blacks Mt. Block 46	28	12-58	24	102	3,311	61	23.5	8,277
Little Schneider—F	33	13-70	43	250	12,540	107	57.4	31,352
Little Schneider—L	32	13-65	50	279	12,800	126	64.0	32,002
Wonder Plot (1943)	26	9-68	194	738	35,533	194	67.8	35,533

[1]A square unit contains 10.89 sq. ft.

TABLE 4. Approximations to parameters of conceptual populations based on point sampling rules applied to compartments F *and* L *of a virgin stand of mixed conifers, Little Schneider Creek, Plumas County, California.*

	K value—compartment F					*K* value—compartment L				
Parameter	20	25	35	40	50	20	25	35	40	50
Expected value										
Number of trees	107	107	107	107	107	126	126	126	126	126
Total basal area	57.00	57.12	57.21	57.24	57.30	63.57	63.66	63.74	63.81	63.85
Total volume	31,347	31,347	31,347	31,348	31,349	31,999	31,999	31,997	31,997	31,995
Variances										
Number of trees										
Total basal area	13,329	9,172	5,489	4,421	3,113	13,489	9,208	5,403	4,424	3,238
Total volume	1,497	1,033	612	489	348	1,824	1,270	777	651	486
(thousand)	481,390	327,298	192,475	157,335	116,302	468,924	329,477	210,001	177,436	130,757
Coefficients of variation										
Number of trees	1.08	.90	.69	.62	.52	.92	.76	.58	.53	.45
Total basal area	.68	.56	.43	.39	.33	.67	.56	.44	.40	.35
Total volume	.70	.58	.44	.40	.34	.68	.57	.45	.42	.36
Correlation coefficients										
No. of trees total basal area	.61	.64	.64	.63	.61	.79	.80	.79	.79	.79
No. of trees, total volume	.42	.45	.46	.44	.43	.67	.67	.66	.66	.66
Basal area, total volume	.96	.96	.96	.96	.96	.97	.97	.97	.97	.97

that the population variance decreases with increasing values of K. The trend of the population variances with changing values K in the two forests is similar. To get a measure of variability in absolute terms, we use the coefficient of variation, the ratio between the standard deviation and the mean. Number of trees turns out to be relatively a more variable characteristic than total basal area or total volume, especially when K is small. The total volume characteristic is only slightly more variable than the total basal area characteristic. The coefficients of variation for total volume and for total basal area agree closely for the two compartments for any given value of K, but those for number of trees differ.

In a human population we might consider the height, weight and age of individuals as three measurement characteristics and expect to find correlations between these attributes of persons. Similarly, we may wish to determine the correlation of one characteristic with another in the elements of our conceptual populations. We may want to consider, for example, the number of trees and the total basal area characteristics of each cluster and calculate

the correlation coefficient.

The results in Table 4 indicate that the correlation coefficients between any two of the three characteristics are independent of the value of K, in the range of K's evaluated. The correlations involving number of trees seem sensitive to differences between the two compartments in tree size and arrangement. The correlation coefficient between basal area and total volume is .96 or higher in both forests. Therefore, the double-sampling proposal of Bell and Alexander (1957), in which a large point-sampling of the basal area characteristic is supplemented by a smaller sample of the volume characteristic, would seem very efficient in stands like these.

Line sampling trials also seem to yield satisfactory approximations to stand volume, basal area, and number of trees (Table 5), with some tendency to small systematic errors showing trends with the value of K used. Study of coefficients of variation suggests some noteworthy differences between line-sampling and point-sampling.

The coefficients of variation for line sampling are much lower than those for point-sampling for a given value of K. This outcome is not surprising since the lines run the entire length of the forest, 5 chains or about 100 meters. In Compartment F, the measure of number of trees by line-sampling is no more variable than measures of basal area and volume, but in Compartment L, number of trees has a higher coefficient of variation. The reduction in variability accomplished by increasing the value of K in line-sampling with lines 5 chains long is very modest. However, the reduced variance which follows an increasing K is more marked in Compartment F than in Compartment L. Differences in stand structure seem to be reflected better in line-sampling by the coefficients of variation of basal area and of volume, than by that of number of trees. This is a reversal of the relationship found for the point-sampling coefficients of variation for these two compartments. The patterns displayed by the correlation coefficients in line-sampling show the same general trends as do those for point sampling, but with a tendency to be less stable over changing values of K.

TABLE 5. Approximations to parameters of conceptual populations based on line sampling rules applied to compartments F *and* L *of a mixed conifer stand, Little Schneider Creek, Plumas County, California.*

Parameter	K value—compartment F					K value—compartment L				
	20	25	35	40	50	20	25	35	40	50
Expected value										
Number of trees	107	107	107	107	107	126	126	126	126	126
Total basal area	57.18	57.21	57.33	57.37	57.42	63.75	63.73	63.85	63.88	63.91
Total volume	31,379	31,371	31,364	31,359	31,357	32,039	32,028	32,018	32,012	32,008
Variances										
Number of trees										
Total basal area	1,215	999	755	699	628	1,509	1,400	1,218	1,138	1,032
Total volume	347	289	225	197	155	194	192	172	159	149
(thousand)	127,144	103,664	79,523	68,862	52,680	47,331	47,479	43,475	38,717	35,364
Coefficients of variation										
Number of trees	.33	.30	.26	.25	.23	.31	.30	.28	.27	.25
Total basal area	.33	.30	.26	.24	.22	.22	.22	.21	.20	.19
Total volume	.36	.32	.28	.26	.23	.21	.22	.21	.19	.19
Correlation coefficients										
No. of trees total basal area	.75	.75	.71	.69	.71	.83	.82	.84	.87	.91
No. of trees, total volume	.68	.70	.65	.61	.61	.72	.70	.72	.75	.81
Basal area, total volume	.99	.99	.99	.99	.99	.97	.97	.97	.97	.97

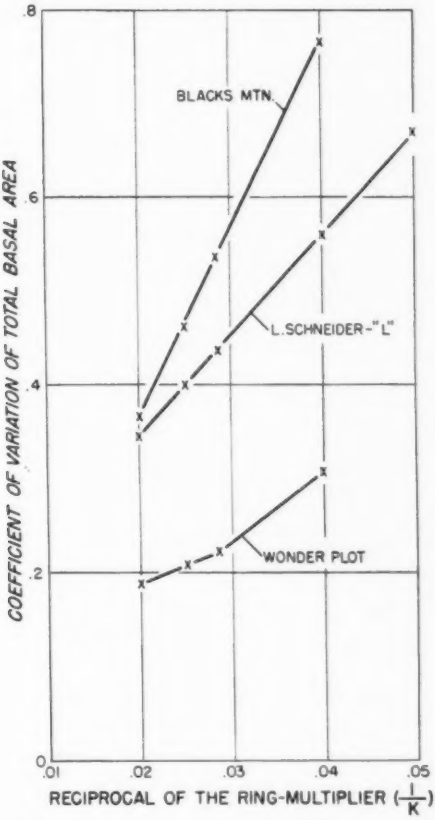

FIGURE 3. *Trends of the coefficient of variation of total basal area over selected values of* K *in three California forests: point sampling.*

To study the influence of changes in the forest on the effectiveness of these two methods of sampling, the computer programs were next applied to forest stands representative of two other California forest regions: the interior ponderosa pine type and the coastal redwood forest. The pine represented lighter, the redwood forest heavier conditions than the mixed conifer type. The Black Mountain stand (Table 3) is typical of the East-side pine type. It consists largely of ponderosa and Jeffrey pines with a small admixture of white fir and incense cedar. We use a 2.5 acre subcompartment measured before cutting. The Wonder plot (Table 3) is a 1-acre stand of young-growth redwoods on the Big River flat in Mendocino County, 85 years of age at the time of the measurements used in this study. This exceptionally well forested acre contains trees of both sprout and seedling origin, with a few large veterans intermingled.[5]

We can now look at coefficients of variation for three contrasting forest types for point sampling and line sampling. At any particular level of K, there is greater relative variability as we move inland towards drier climatic regions and stands containing fewer trees and lower volumes and basal areas (Table 6). This finding is consistent with the general view of the relative variability of these forests under plot sampling. In all of these stands the

[5]The help of D. Gordon and Professor Emanuel Fritz in supplying maps and measurements of Blacks Mountain and of the Wonder Plot, respectively, is gratefully acknowledged. Volumes by standard volume table in Blacks Mountain, local volume table in Wonder Plot.

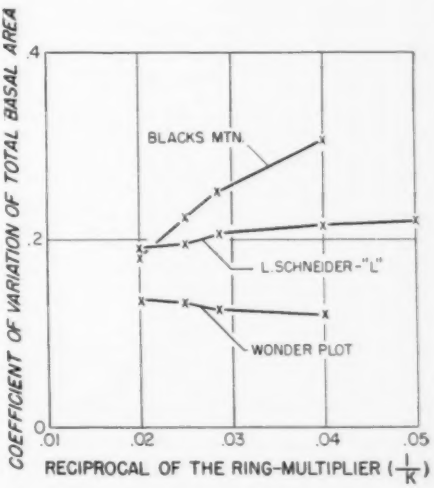

FIGURE 4. *Trends of the coefficient of variation of total basal area over selected values of* K *in three California forests: line sampling.*

relative variability of number of trees is greater under point sampling than the relative variability of total basal area and total volume.

It is instructive also to look at the relationship between population variance and the value of K, based on the results from four stands and five levels of K. Within the range of values of K that were tried, population variance tends to be proportional to the reciprocal of K^2. We may look at this relationship graphically in Figures 3 and 4 where coefficients of variation of total basal area for three of the stands are plotted over the reciprocal of K for each of the values of K examined. The relationship for point sampling for the Wonder plot is linear in the range of K from 35 to 50, but not in the full range from 25 to 50. It follows from our generalization that within an effective range, increases in K will lead to reductions in the coefficient of variation. Nevertheless, it is very necessary to remember that the number of trees selected and therefore the amount of work to be done in point-sampling will go up as K^2.

Correlation coefficients between basal area and volume are very high for all instances of point and line sampling. This result reflects the high correlation between the basal area and volume of the underlying population of trees making up the forests. The correlations between number of trees and basal area are in all cases higher than those between number of trees and volume. There is greater variability in these correlation coefficients as we go from forest to forest. Here again we see an indication of the fact that a sampling method which selects trees with probability proportional to basal area (or to diameter in the case of line sampling) is likely to result in a characteristic relating to number of trees which, while unbiased, may have relatively high variability.

TABLE 6. Results of simulated point and line sampling trials in four California forests for various values of K.

	Coefficient of variation						Correlation coefficients					
							Point Sampling			Line sampling		
	Point sampling			Line sampling			No. of	No. of		No. of	No. of	
Name of forest	No. of trees	Basal area	Volume	No. of trees	Basal area	Volume	trees B.A.	trees Vol.	B.A. Vol.	trees B.A	trees Vol.	B.A. Vol.
					$K = 25$							
Blacks Mountain	1.15	0.77	0.86	0.34	0.31	0.29	0.67	0.46	0.92	0.66	.	0.94
Little Schneider—F	.90	.56	.58	.30	.30	.32	.64	.45	.96	.75	70	.99
Little Schneider—L	.76	.56	.57	.30	.22	.22	.80	.67	.97	.82	.70	.97
Wonder (1943)	.52	.31	.32	.14	.12	.12	.63	.47	.95	.73	.70	.96
					$K = 35$							
Blacks Mountain	0.84	0.54	0.60	0.27	0.25	0.26	0.64	0.42	0.92	0.55	0.42	0.93
Little Schneider—F	.69	.43	.44	.26	.26	.28	.64	.46	.96	.71	.65	.99
Little Schneider—L	.58	.44	.45	.28	.21	.21	.79	.66	.97	.84	.72	.97
Wonder (1943)	.39	.22	.22	.10	.13	.12	.62	.43	.94	.73	.71	.98
					$K = 40$							
Blacks Mountain	0.74	0.46	0.51	0.25	0.23	0.24	0.63	0.40	0.91	0.47	0.33	0.92
Little Schneider—F	.62	.39	.40	.25	.24	.26	.63	.44	.96	.69	.61	.99
Little Schneider—L	.53	.40	.42	.25	.19	.19	.79	.66	.97	.91	.81	.97
Wonder (1943)	.36	.21	.21	.10	.13	.13	.60	.42	.95	.75	.72	.99
					$K = 50$							
Blacks Mountain	0.62	0.37	0.39	0.22	0.18	0.20	0.63	0.40	0.91	0.42	0.22	0.90
Little Schneider—F	.52	.33	.34	.23	.22	.23	.61	.43	.97	.71	.61	.99
Little Schneider—L	.45	.35	.36	.25	.19	.19	.79	.66	.97	.91	.81	.97
Wonder (1943)	.29	.19	.19	.09	.14	.14	.53	.35	.96	.85	.85	1.00

Insights into point sampling and line sampling. We are now ready to summarize what we have learned about the point and line sampling methods of forest sampling from the applications of the computer technique to date. In directing our comments more specifically to actual sampling situations involving samples of elements from the conceptual populations, we will speak of the properties of the estimates made from samples, rather than of the properties of the elements themselves. The following list of statements seems to us to sum up our initial findings:

1. For a fixed size of sample and for values of K from 20 to 50 in forests like those described reductions in the relative variability of estimates (the "sampling error") can usually be brought about by increasing the value of K. The cost of so doing must be considered along with the physical feasibility of defining the clusters of trees without error.

2. To attain a given level of sampling error a larger value of K will be required in a stand of few trees and low basal area than in a stand of many trees and high basal area.

3. Point sampling estimates of number of trees will show considerably more relative variability than point sampling estimates of basal area and volume.

4. Line sampling estimates of number of trees show no more relative variability than do line sampling estimates of basal area and volume. We suggest that line sampling may have relevance in surveys of pole-timber and insect-infested trees, and in other surveys where number of trees is the important variable and large areas must be covered.

5. The correlation coefficient between basal area and volume estimates based on point or line sampling is high, probably .9 or greater. This value remains constant over a fairly wide range of sampling angles. In irregular or multistoried stands a lower correlation might be found.

6. The correlation coefficient between point sample estimates of number of trees and of basal area seems to be sensitive to changes in tree arrangement and size. This correlation measure warrants further investigation as a means of quantifying differences in the spatial distribution of trees.

The Future of This Technique

The idea of putting forests into the memory of a computer and then simulating the application of different rules of sampling has promise in relation to those problems of forest sampling which can best be approached, in terms of a study of all possible samples or a reasonable approximation of all possible samples. Once the basic labor of mapping and measuring the forests has been accomplished, the number of rules of sampling which can be evaluated is incomparably greater than could be done readily in any other way. By adding small forests together and by using computers of greater memory capacity, larger forests than those treated here might be dealt with. In such forests it is probable that interesting comparisons can be made between random and systematic sampling designs, an important area where both theoretical and empirical knowledge is scarce.

An important extension of this technique which the authors hope to program for the IBM 704 installation on the Berkeley Campus of the University of California is the study of plot samples of various sizes. This would be done with the particular intention of comparing plot samples with point samples in terms of their precision and efficiency. Further, it is believed that the effect of the spatial distribution of trees on the populations defined by sampling rules can be studied using this technique, either by generating imaginary forests or by rearranging the trees in some of the natural stands already dealt with.

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The Conifers

Die Nadelgehölze. By Berd Krüssmann. 335 pp. Illus. Paul Parey, Berlin (SW 61, Lindenstrasse 44-47) and Hamburg. 1960. Price about $18.

Review by Elbert L. Little, Jr.
Forest Service, U. S. Department of Agriculture

Publication of the second edition only five years after the first is evidence of the popularity of this practical reference on the needleleaf trees and shrubs of conifers. The subtitle summarizes the contents as a systematic survey and alphabetical list with descriptions and evaluations of the conifers hardy in Middle Europe, including some species and forms not hardy. This is the successor to the earlier Handbuch der Nadelholzkunde by Ludwig Beissner, for many years a standard German reference.

The author is dendrologist and director of the Botanical Gardens at Dortmund, Germany. He has written also two handbooks on tree nurseries and planting and the first of two volumes of a companion reference on broadleaf trees, Handbuch der Laubgehölze (1960). During the interval since the 1955 edition, he traveled widely in the United States and Canada as well as in Europe for additional study of wild and cultivated trees.

The introduction contains short taxonomic descriptions of the families and genera treated. The classification of conifers by Rudolf Florin, of Stockholm, was adopted also in the first edition. Keys are lacking, but large genera have tables comparing important characteristics of the different species.

Botanical descriptions of the genera and 350 species are followed by shorter descriptions of 1133 cultivated varieties (cultivars) or horticultural forms. Scientific names agree with the latest usage under the International Code of Botanical Nomenclature. The second edition conforms also to the new International Code of Nomenclature for Cultivated Plants and accordingly distinguishes names of cultivated varieties in single quotation marks.

The 439 figures, mostly assembled from other sources, include habit photographs of wild and planted trees, drawings of cones and foliage for identification, and interesting small world maps showing distribution of genera. (Before the next edition revised distribution maps of the United States species will be available for correction of minor errors.) The number of figures is 67 greater than in the first edition, and there are 31 more pages.

This edition adds a map of southern and western Europe showing hardiness zones based on average minimum annual temperatures. The hardiness zone of each species is indicated. Also, the horticultural value is rated by symbols.

The book closes with a list of important collections of conifers or pineta. To the five mentioned from the United States, the reviewer would add the Eddy Arboretum, of the Institute of Forest Genetics, Placerville, Calif.

Probably the chief uses in the United States for this accurate, well illustrated reference will be for identification and selection of ornamental conifers. Foresters engaged in tree improvement programs will find here the exotic conifers available for introduction and hybridization. For those with limited knowledge of the German language the names, illustrations, and symbols are self-explanatory.

Forestry Theses Accepted by Colleges and Universities in the United States

Supplement July 1959-June 1960 Including Additions for July 1958-June 1959

Compiled by
KATHERINE H. OSBORN

Subject Index by
RAY A. YODER
WILLIAM I. WEST

A LIST of forestry theses for January 1956-June 1958 was published in *Forest Science*, Volume 5, Number 3, September, 1959. Information is given there on availability of earlier lists and lists covering related subjects.

The list for July 1958-June 1959 was published in *Forest Science*, Volume 6, Number 3, September, 1960.

The list of forestry theses for this supplement presented alphabetically by institutions follows.

Auburn University

1960

1. Lewis, Arnold David. Some responses of loblolly pine seedlings grown in nutrient-sand culture to varied concentration of the major cations.

University of California

1958

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